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JOURNAL
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ARNOLD ARBORETUM

VOL. XXXV JANUARY 1954 NUMBER 1

STUDIES IN THE BORAGINACEAE, XXVI
FURTHER REVALUATIONS OF THE GENERA OF THE LITHOSPERMEAE

IVAN M. JOHNSTON

PREPARATORY TO A GENERAL DISCUSSION of the Lithospermeae to be published in the near future, seventeen genera of the tribe are given individual treatment in the present paper. These, along with six genera discussed previously, Jour. Arnold Arb. 34: 258–299 (1953), include all the genera which can be referred to the tribe if that is to be a homogeneous division of the Boraginoideae. Of the seventeen genera here discussed only one, *Lithospermum*, has representatives native to both America and the Old World or has direct relations with genera in both regions. Since the distribution and relationships of all other genera are confined within one or the other of these major regions, the primary division in my key to the genera has been deliberately based on geography. For most uses this will be a convenience. Furthermore, it also has the advantage of permitting sharper contrasts of immediately related genera. A synopsis of all the genera of the tribe and technical keys for their identification will be provided in the following paper of this series.

KEY TO THE GENERA

PLANTS NATIVE TO AMERICA.

Anthers completely exserted from the throat; filaments elongate, 6–70 mm. long, exserted 1–65 mm. from the corolla mouth; corolla large, 39–90 mm. long, trumpet-shaped, lobes usually ascending or recurved or reflexed; pollen ellipsoidal to ovoid or ovoid-oblong, 23–33 × 15–28 μ . . . . 1. **Macromeria.**

Anthers completely included in the throat or only partially exserted from the corolla mouth; filaments at most 10 mm. long and usually very much shorter, completely included or exserted less than 1 mm.; corolla smaller, usually less than 25 mm. long and never more than 50 mm. in total length, tubular to salverform, lobes erect to spreading.

Flowers precociously sexual, corolla opening and exposing stamens and style before attaining full size; corolla-lobes erect, sharply acute or acute with an attenuate tip, very narrowly imbricate in the bud, usually evidently longer than broad; sinus between the corolla-lobes plicate and inflexed and thickened at the base; pollen ovoid, 16–24 × 13–22 μ. . . . 2. **Onosmodium.**

Flowers not precociously sexual, corolla opening only when fully developed; corolla-lobes obtuse or rounded, frequently as broad as long or even broader than long, broadly imbricate in the bud; sinus between the corolla-lobes neither plicate nor thickened nor inflexed at the base.

Filaments about half the total length of the corolla, twice as long as the anthers, arising low in the corolla, towards the base shaggy with slender multicellular gland-tipped hairs; anthers borne high in the corolla-throat with its sterile tip exserted; tip of anther 1–2 mm. long; pollen ovoid, 25–28 × 21–33 μ. ..... 3. **Nomosa.**

Filaments less than a third of the total length of the corolla and usually much shorter than the anther, usually arising at or above the middle of the tube, glabrous or bearing only a few inconspicuous stipitate glands; anthers without a sterile tip or the tip less than 1 mm. long.

Filaments broadening upwards from a narrow attachment; anthers with a small but definite sterile tip, with a well-developed sinus at the base.

Corolla lacking faucal appendages, corolla-lobes deltoid; filaments oblanceolate, almost as long as the anthers; anthers conspicuously hairy on the back, with an erect tip, thecae without darkened margins; pollen ovoid, 20–23 × 16–20 μ; coarse plant with broad strongly veined leaves ..... 4. **Lasiarrhenum.**

Corolla with evident faucal appendages; corolla-lobes rounded; filaments triangular or obovate-triangular, half as long as the anther; anther glabrous, with a recurved tip, thecae with darkened margins; pollen ellipsoid, 24–25 × 20 μ; small slender-stemmed plant with very narrow veinless leaves ..... 5. **Perittostema.**

Filaments linear or subulate or unguiculate; anther only very rarely bearing a sterile tip, base emarginate or rounded.

Corolla-throat angulate, externally with a small swelling directly below each sinus; corolla-lobes strictly ascending; filaments partially exserted from the throat; anthers one half to three fourths exserted from the throat; inside of corolla completely glabrous and bearing neither faucal appendanges nor stipitate glands; style exserted; pollen ellipsoid, 23–26 × 16–22 μ. ..... 6. **Psilolaemus.**

Corolla-throat not angulate, not swollen externally below each sinus of the limb; corolla-lobes usually spreading; filaments and anthers always included in the throat; corolla inside with faucal appendages or stipitate glands or both and sometimes hairy; style usually included; pollen diverse as to size and form ... 12. **Lithospermum.**

PLANTS NATIVE TO THE OLD WORLD.

Anthers without a sterile tip or with the tip small and inconspicuous and rising abruptly from the emarginate, truncate or rounded summit of the anther; base of anther usually rounded or simply emarginate; base of theca not pointed, usually rounded; anthers always distinct, never joined together; pollen inconspicuously if at all colpate, pores in one or sometimes two rows, 6–9 or more.

Nutlets narrowed upwards into a prolonged beak, conspicuously rostrate with the apex hamate; cymes bractless above the base; upper leaves very ample and evidently veined; corolla-throat inside abundantly and antrorsely villose-strigose; Japan ..... 7. **Ancistrocarya.**

Nutlets not conspicuously rostrate, apex not hamate; cymes bracted through-

out; upper cauline leaves not conspicuously ample, usually veinless; corolla-throat inside not villose-strigose.

Corolla-throat inside bearing 5 well-developed elongate vertical guide-lines for insect visitors; guides consisting of vertical inflexed plaits bearing hairs or stipitate glands or both, or consisting merely of elongate vertical bands of crowded hairs and stipitate glands; anthers usually with small sterile tips; style usually with a prolonged bilobed sterile apex, always short, always shorter than the mature nutlets . . . . . 8. **Buglossoides.**

Corolla-throat lacking guide-lines, bearing localized faucal appendages or bearing stipitate glands which are scattered or are in localized congregations, or sometimes naked; anthers only very rarely bearing a minute sterile tip; style only very rarely with a prolonged bilobed sterile apex, short to elongate, usually becoming much longer than the nutlets.

. Nutlet attachment not on the true base of the nutlet, borne ventral to the nutlet base at the lower end of a stipe which is directed downward from the ventral side of the ascending nutlet-body; pollen with biseriate pores; Mongolian . . . . . 9. **Stenosolenium.**

Nutlet attachment on the base of the erect nutlet-body.

Pollen bearing 2 rows of pores, one about each end of the elongate grain, grains oblong or medially constricted, upper and lower halves of the same size and configuration; corolla without faucal appendages, its inner surfaces prevailingly devoid of stipitate glands, such glands when present scanty, inconspicuous, and confined to the corolla mouth; flowers heterostylic or monomorphic; stamens usually whorled, affixed at unequal heights above the corolla base only in one monomorphic species; Asia extending into Africa . . . . . 10. **Arnebia.**

Pollen bearing a single row of pores either about the equator or below the equator about the lower half of the grain; grains globose, oblong-ellipsoidal or with the upper and lower halves dissimilar in size and configuration.

Corolla inside without faucal appendages or stipitate glands; annulus absent; stamens borne at very unequal heights on the corolla-tube; flowers heterostylic; Caucasus, Armenia, and adjacent Iran . . . . . 11. **Echioides.**

Corolla inside with faucal appendages or stipitate glands or both; annulus present; stamens whorled, all borne at the same level above the corolla base; flowers heterostylic or monomorphic; Eurasia, Africa, and America . . . . . 12. **Lithospermum.**

Anthers narrowed into a prolonged evident sterile tip; base of anther usually with an open sinus and hence somewhat sagittate; basal tip of theca usually pointed or narrowly prolonged; anthers usually joined to form a synandrium; pollen evidently colpate, pores in a single row.

Nutlets bilocular; calyx-lobes very unequal, strongly imbricate; anthers distinct or joined by the entangling of the tail-like appendages borne at the base of the theca; pollen barrel-shaped or ellipsoidal, pores 8, borne in a well-developed equatorial groove; plant nearly glabrous, leaves with a cordate-amplexicaul base . . . . . 13. **Cerinthe.**

Nutlets unilocular; calyx-lobes equal or practically so, not imbricate; anthers usually coherent at the base or along the sides or both; pollen ovoid or

globose or cylindric or ellipsoidal, pores 3, suprabasal or equatorial, not in an equatorial groove; plants evidently hairy, middle or lower leaves never with a cordate-amplexicaul base.

Nutlets bent 90° below the middle, strongly incurved, attachment small and substipitate appearing to be lateral but actually basal on the short erect lower section of the nutlet; gynobase with elevated pulvinate lobes each bearing a small attachment face; indument on herbage with intermixed slender gland-tipped hairs; bracts becoming large and foliaceous; fruiting calyx frequently on decurved pedicels . . . . . 14. **Podonosma.**

Nutlets straight and erect or nearly so, with a usually broad and evidently basal attachment; gynobase not bearing the attachment faces on elevated pulvinate lobes; indument containing no gland-tipped hairs; bracts rarely becoming conspicuous and foliaceous; fruiting calyx borne on erect or ascending pedicels.

Corolla-lobes well developed, as long as or much longer than the tube, spreading or decurved; anthers coherent only along the margins of the terminal appendage, the appendage evidently longer than the theca; filaments very short and usually bearing a hairy basal appendage; throat of corolla frequently hairy; southern Arabia, Socotra, Somaliland to Angola . . . . . 15. **Cystistemon.**

15a. **Vaupelia.**

Corolla-lobes short, commonly about as long as broad, conspicuously much shorter than the tubular part of the corolla, erect or loosely recurved (or, in one species, *Onosma longilobum*, with the lobes elongate, longer than the tube, but erect); anthers usually coherent at the base and frequently also along the margins of the thecae and the appendages, the appendage almost always shorter than the theca; filaments usually elongate, not appendaged at the base; throat of corolla never with spreading hairs; North Africa and Europe to eastern Asia.

Calyx-lobes narrow and elongate, more or less parallel, separated by a very narrow or closed sinus; corolla having no puffed-out ribs projecting between the calyx-lobes; filaments within a corolla all similar; anthers included to completely exserted from the corolla; nutlets smooth to rough with the surface only very rarely evidently papillate or muriculate; pollen ovoid to spheric or transversely ellipsoid . . . . . 16. **Onosma.**

Calyx-lobes more or less triangular, ascending, separated by an open triangular sinus; corolla with puffed-out ribs projecting between the calyx-lobes; filaments within a corolla differing in the shape of their base and in the orientation of their attachment on the corolla; anthers included; nutlets roughened and with the surface abundantly and minutely papillate or muriculate; pollen cylindric or vertically ellipsoid; Himalaya and mountains of southwest China. . . . . 17. **Maharanga.**

1. **Macromeria** D. Don, New Edinb. Philos. Jour. 13: 239 (1832). Based upon *M. longiflora* Don and *M. exserta* Don.

Philonomia DC. in Steud. Nom. ed. 2, 2: 320 (1841); Meisner, Pl. Vasc. Gen. 2: 189 (1836–43), in synom.

Onosmodium § *Macromerioides* Gray, Synop. Fl. N. Am. 2[1]: 205 (1878). Type species, *Macromeria viridiflora* A. DC.

Macromeria § *Macromerioides* (Gray) Johnston, Contr. Gray Herb. **70:** 13 (1924).

Plant perennial. Stems coarse, erect, simple or bearing a few leafy fertile branchlets in the upper axils, hispid or sometimes hispid-villose or strigose. Leaves well developed, all cauline, lowest ones smaller than the upper, hispid, velvety or strigose (hairs on upper surface usually with discoid or bulbose bases), with evident midrib and usually two or more pairs of well-developed evident assurgent veins. Cymes scorpioid, simple or sometimes geminate, terminating the main stems and frequently also arising directly from the uppermost leaf-axils and sometimes terminating leafy branchlets arising from the upper axils, relatively loose, with the flowers not evidently biseriate, after anthesis becoming straight, very loosely flowered, and very elongate; bracts numerous, conspicuous and foliaceous, usually somewhat accrescent in age, lanceolate to broadly ovate. Flowers at anthesis borne on strict pedicels at the summit of the straightened portion of the cyme and hence erect, or borne on the still curved portion of the cyme and directed backwards over the top of the cyme with the abaxial side uppermost and the corolla accordingly resupinate. Calyx 5-fid, the lobes elongate, usually evidently unequal, linear to narrowly lanceolate; pedicels elongating at maturity, strict or ascending. Corolla yellow, yellowish or greenish, straight and regular or curved and having the throat prolonged on the two-lobed adaxial side, elongate, somewhat trumpet-shaped, having a slender tube which gradually or abruptly expands into an elongate, subcylindric or conic-cylindric throat once to twice as long as the tube, the outer surface always evidently hairy, the inner surface glabrous or rarely inconspicuously hairy in the tube and on the lobes and along the veins in the throat, usually glanduliferous in the throat and sometimes on the lobes; faucal invaginations evident in one species but usually absent or only very obscurely developed, when present decorated with glands. Annulus absent or represented by a very narrow, continuous or interrupted lineate ridge just above the base of the tube, glabrous, or in one species with very inconspicuous tufts of minute hairs. Corolla-lobes equal, elliptic to deltoid, erect to ascending or reflexed at the base or rarely loosely recurved, shorter than the throat, imbricate, apex tending to be acute. Filaments equal, terete or distinctly flattened or even strap-shaped, glabrous or somewhat hairy in one species, arising well above the middle of the corolla-throat and always exserted from it but in only one species extruded more than the length of the corolla-lobes, affixed all at the same altitude on the corolla or at three superimposed levels with the medial adaxial one highest, the abaxial pair lowest, and the adaxial laterals at an intermediate level. Anthers straight or sometimes weakly falcate, elongate, oblong or oblong-linear, several to many times shorter than the filaments, affixed at or slightly below the middle, commonly in a groove in the connective, strict and erect or becoming horizontal by a subapical bend of the filament or sometimes versatile, apex usually rounded or obtusish and with a small inconspicuous tip formed by the prolongation of the connective tissue, but in one species emarginate and bearing a subapical gland; thecae parallel

but unjoined for a short distance above the unappendaged, apparently emarginate base of the anther; connective evident on the back of the anther, especially above the middle, glabrous or in one species bearing short stout hairs above the middle. Pollen broadly to narrowly ellipsoidal or somewhat ovoid or ovoid-oblong, 25–33 × 15–28 μ, sometimes constricted near the middle, upper and lower half of the grain equal or more or less dissimilar, pores borne eight or nine in a single row at the equator or below it and sometimes very low on the grain just above its rounded base, grain in polar profile circular or obscurely polyhedral. Style filiform, glabrous, longer than the corolla and becoming evidently exserted; stigmas two, very small, juxtaposed and terminal on the tip of the style or subterminal and separated (though scarcely if at all surpassed) by an apical prolongation of the style. Nutlets smooth, ovoid or ellipsoidal, usually smooth, lustrous and white, straight, erect or more commonly diverging from the pyramidal gynobase; ventral keel weak or absent, suture completely closed or represented (sometimes only on the upper half of the nutlet body) by a lineate groove; attachment scar broad, basal, flat or convex, usually bearing the projecting end of the tubular bony funicular canal. Gynobase somewhat pyramidal, usually broadly so and commonly terminated by the thickened four-angulate base of the style; attachment faces nearly as broad as long, at maturity each surrounded by an elevated cartilaginous margin, usually sloping and the basifixed nutlets borne upon them usually divergent.

A genus obviously related to *Lithospermum* and most closely so to its Mexican species. It is distinguished only by the form and large size of its corollas and by having filaments elongate and exserted from the corolla-throat. Its eight species are well marked and form a very natural assemblage. They range between northern Guatemala and Arizona and New Mexico in southwestern United States, with most of them confined to very restricted areas in the mountains of Mexico.

Macromeria, as originally defined and established by David Don, included two species, *M. longiflora* and *M. exserta*. The most detailed subsequent treatments of the genus have been by De Candolle, Prodr. **10**: 68 (1846) and by Johnston, Contr. Gray Herb. **70**: 13 (1924). Of the species which have been referred to the genus, only *M. cinerascens* DC. (1846) is to be excluded, that being a species of *Lithospermum*. Both Gray, Synop. Fl. N. Am. 2[1]: 205 (1878), and Macbride, Contr. Gray Herb. **49**: 19 (1917), have suggested that the genus should be reduced to one species, *M. exserta*, and that the remaining species be treated as a section of *Onosmodium*. As previously noted by me, Contr. Gray Herb. **75**: 16 (1924), such procedure would do violence to natural relationships by separating *M. exserta* from its evident relative *M. hispida*. It would also destroy the homogeneity of *Onosmodium*. The eight species of *Macromeria* are obviously more closely related to one another than any of them are to any species of *Lithospermum* or *Onosmodium*. From the latter genus they differ in size and form of the corolla, length of filaments, shape of the anthers, and tardily exserted style.

The species of this genus are coarse perennials having few to numerous stems usually over half a meter tall and frequently approaching and rarely even surpassing a meter in height. The leaves are all cauline, the lowermost being smaller and proportionately more elongate than those on middle sections of the stem. The leaf-blades have a strong midrib and also several well-developed assurgent lateral veins. In foliage, as well as in general habit, *Macromeria* is suggestive of *Onosmodium* and *Lasiarrhenum*, and to a somewhat less degree also of such American species of *Lithospermum* as *L. viride*, *L. oblongifolium*, *L. guatemalense*, and *L. cinerascens*.

The corollas, 35–90 mm. long, are among the largest in the Boraginaceae, with those of *M. exserta* the very largest in the family. They are more or less trumpet-like in form, having an elongate subcylindric or conic-cylindric throat usually several times longer than thick and commonly about as long as the slender tubular portion of the corolla supporting it. The equal, relatively short lobes are ellipsoidal, deltoid, or triangular ovate and commonly pointed. They may be straight and ascending or loosely recurving or abruptly reflexed at the base. In most of the species the corolla is regular or practically so, but in *M. hispida* and *M. exserta* it is curved, the throat is oblique and evidently prolonged on the adaxial side, and the stamens are affixed at superimposed levels in the throat, with the adaxial medial member highest. The corolla in these two species having a very distinct bilateral symmetry is clearly zygomorphic. This condition is usually most obvious in the bud of the corolla just before it opens. For most of its length the bud is gracefully curved adaxially, but in the thickened apical portion it becomes curved in the reverse direction. The outer thickened portion of the bud, formed of the unexpanded lobes, is evidently swollen on the two-lobed adaxial side. The bud has its tip not central but closest to its abaxial side. These zygomorphic corollas of *M. exserta* and *M. hispida* have their two-lobed lip and their medial stamen both on the adaxial side of the flower.

In most species of the genus, both before and after anthesis, the corolla stands erect, being borne on strict pedicels at the summit of the straightened portion of the cyme. In *M. hispida* and *M. exserta* the corolla at anthesis, and also as a mature bud, is borne at a relatively higher position on the scorpioid cyme, mostly developing on the curve between its arched summit and the point at which it becomes straight and vertical. Since the pedicels are strict and borne on the curved portion of the cyme, the flowers are directed ascendingly backwards over the arched top of the cyme. The backward direction of the flowers in *M. exserta* is given further accentuation by the marked adaxial curving of the throat and tube. As a combined result of all this, at anthesis the outer parts of the corolla achieve a nearly horizontal position. By leaning backwards over the tip of the cyme the corolla has become resupinate.

The corolla in all species except *M. viridiflora* bears at least scattered stiped glands in the upper parts of the throat and usually also on the adjacent portions of the lobes as well. In *M. leonotis* the salient mouth of

the corolla is encircled by a band of glands. In species such as *M. barbigera*. *M. hispida*, and *M. exserta*, the glands are more scattered, less evident, and may be distributed from above the level of the filament attachments upward onto the lower half of the corolla-lobes. In *M. Pringlei* and less clearly in *M. longiflora* the glands are restricted to obscure congregations associated with small, weak, ill-defined circular or elliptic convexities, one located at or slightly below each of the corolla-lobes. In *M. notata* the association of glands and invaginations is much clearer. In that species there are five inflexed plaits, cuneate in outline, which have their broad end (1–1.5 mm. wide) about 2 mm. below the summit of the throat, and from thence, gradually narrowing, extend outward along the midline of each corolla-lobe with their pointed end about 2 mm. below the lobe apex. Stipitate glands are abundant on these elongate swollen areas but practically absent elsewhere on the corolla. A unique feature of *M. viridiflora* is the presence of minute hairs on the inner surface of the corolla. The corolla is villulose inside the slender tube and may be scantily and minutely strigulose below the middle of the throat along the vein leading from each corolla-lobe. Though hairy the corolla bears no glands.

The corollas of *Macromeria* have no annulus or at most only a weakly developed one ca. 0.5 mm. above the base of the tube. In *M. notata* the annulus is represented by an inconspicuous narrow encircling ridge, and in *M. barbigera* by an obscurely five-lobed one, but in all other species it is obscure or absent. Hairs, these very minute and inconspicuous, were noted in association with the annulus only in *M. leonotis*.

The stamens are affixed in the corolla-throat and within an individual flower are all at about the same distance (4–10 mm.) below the base of the corolla-lobes. In regular corollas the filaments arise at equal distances above the corolla-base. In zygomorphic corollas, however, the throat is prolonged on the adaxial side and the mouth of the throat is oblique. Because the stamen attachments have a fixed relation with the summit of the throat, those on the prolonged adaxial side of the corolla accordingly have a position at a greater distance above the corolla-base than those on the abaxial side. This is the condition in *M. exserta* and *M. hispida*.

The filaments are well developed. In *M. exserta* they may become 70 mm. long, and accordingly are very conspicuously long-exserted from the corolla. The shortest ones (6–9 mm.) occur in *M. notata*. In other species, however, the filaments are mostly 10–20 mm. long. They are clearly exserted from the corolla-throat but do not surpass the corolla-lobes when the latter are in an erect position. In most species the filaments are slightly compressed. In *M. viridiflora*, however, they are strongly so, being strap-shaped, 1.2–1.5 mm. broad just above their base, and then gradually narrowed upwards to become 0.5–1 mm. wide at the apex. In *M. leonotis* the filaments may be sparsely hairy below their middle and sometimes also on their decurrent bases, but in all other species they are always glabrous.

The anthers are elongate and have an oblong outline. They are affixed to the filament at or perceptibly below the middle, usually in an elongate depression in the connective. Although past authors have stated that they

are usually versatile, that condition exists, if at all, only in *M. exserta*. In *M. hispida*, *M. longiflora*, *M. Pringlei*, and probably *M. leonotis* also, the anther may assume a position at right angles to the filament, but that appears to be the result of a ninety-degree bend of the filament just below its apex. In *M. viridiflora* and apparently also in *M. barbigera* the anthers are strictly and firmly affixed to the filament and are erect. The connective is glabrous in most species, but in *M. viridiflora*, in which the structure reaches its maximum development, it may bear numerous stout hairs on the back side of the anther above the middle. In most species the connective is slightly prolonged to form a minute, usually thickish, truncate or subulate apicule on the broad summit of the anther. In *M. viridiflora* the connective is thickened, apparently glandular, and locally very hairy just below the anther tip. It is not prolonged beyond the thecae. The anthers in this species, accordingly, are emarginate at the tip.

The connective is not only broadest but also most readily observed in *M. viridiflora*, *M. Pringlei*, and *M. longiflora*. In these species the thecae, after shedding pollen and becoming explanate, are displayed obliquely on the ventral side of the anther. The back side of the anther is nearly plane, and the broad connective and the filament attachment are fully exposed to view. In the five other species of the genus, however, the explanate thecae have reflexed lower halves, and their surfaces become parallel and face left and right in opposite directions. Such mature anthers are strongly compressed laterally. Their back appears to be strongly conduplicate with the narrow connective and the filament attachment hidden in the depth of the fold.

The style is filiform and sufficiently elongate to bear its stigmas commonly about 5 mm. beyond the anthers. The minute stigmas are subterminal, being separated and surpassed by the tip of the style in *M. Pringlei*, *M. leonotis*, and *M. notata*, but in the other species they are terminal and juxtaposed upon the apex of the style.

As in most other genera of the Lithospermeae, in herbarium specimens I have found the anthers of *Macromeria* dehiscent and the pollen shed in those flower-buds in which the corolla is nearly ready to open. Just previous to the opening of the corolla, the stigma in seven of the eight species is pushing against the very top of the bud-cavity, and hence is above the anthers. The stamens have attained almost full development before the corolla opens. In *M. exserta*, however, the very elongate, eventually long-exserted filaments and style are not completely lengthened before the corolla expands. The filaments have their middle portion lying pressed against the curve of the swollen adaxial side of the outer half of the bud. At the tip of the bud cavity the distal portion of the filaments curves backwards for 180° to 360°. The anthers usually lie within the adaxial half of the most ample part of the bud cavity. The style, shortened by undulate contortions, bears its stigmas appressed against the tip of the bud cavity or against the abaxial side of the cavity close to the tip. In *Echium*, in which elongate filaments and style are also curved and contorted inside the flower bud, the stigmas before the corolla opens may have a position

amidst the clustered dehiscent anthers. In the bud of *Macromeria*, however, the stigmas have a position above or beyond the anthers and so decidedly less accessible to any pollen set free in the bud. The stigma is not precociously exserted. It escapes from the flower bud only when the imbricate corolla lobes have begun to loosen — just before the corolla opens, or, in many cases, not until the corolla is almost completely open.

Macromeria has pollen similar to that of *Lithospermum*, and especially like that of the Mexican members of that genus. Each species of *Macromeria* has distinctive pollen with the grains recognizable if not by shape at least by size. Related species agree more closely in the length of their grains than in the form of them.

The pollen bears eight or nine pores in a single row. Its pores are frequently detectable as minute swellings on the outline of the grains when the latter are viewed in lateral profile. Frequently they are sufficiently prominent to give the sides of the grains a somewhat obtusely angled silhouette. The polar profile of the grain is usually circular, and only very rarely are the pores sufficiently evident to produce a vaguely polyhedral outline. Evidences of possible shallow furrows on the grain have been detected only in *M. barbigera*. The pores are equatorial, and the upper and lower halves of the grain are equal in *M. leonotis* (grains globose ellipsoidal, sides angulate, 25–26 × 23 μ), *M. barbigera* (ellipsoidal, sides rounded or angled, 30–33 × 25–28 μ), *M. notata* (ellipsoidal, sides tending to be angled, 28–30 × 23–25 μ), and *M. Pringlei* (ellipsoidal, sides rounded to nearly parallel, 25–26 × 15–18 μ). In two species, *M. exserta* and *M. hispida*, the grains bear the pores very slightly but still perceptibly below the middle. The lower half of the grain has a more evenly and broadly rounded curve than the upper half. *Macromeria exserta* has ovoid-ellipsoid grains (38–41 × 25–28 μ), and *M. hispida* globose-ovoid grains (38–41 × 33–37 μ). The pollen of the two remaining species of the genus is elongate, perceptibly constricted below the middle, and bears its row of pores above its broad rounded base, where its diameter is greatest. Constrictions of the grain begin directly above the row of pores and form "shoulders" of a type previously noted in grains of a similar type in *Lithospermum*, cf. Jour. Arnold Arb. 33: 310 (1952). Such elongate, medially constricted grains are characteristic of *M. longiflora* (25–28 × 16–18 μ) and *M. viridiflora* (28–33 × 18–22 μ). Of these two species with constricted pollen, *M. viridiflora* has no close relatives. *Macromeria longiflora*, however, is obviously most closely related to *M. Pringlei* and species having ellipsoidal grains with equatorial pores. The only agreement is in the length of the grains.

The nutlets of *Macromeria* are smooth, shiny, and usually white, and are symmetric or nearly so and nearly circular in transverse section. In general appearance they closely resemble those of most American species of *Lithospermum*. The venter of the nutlet is only obscurely if at all keeled. The ventral suture may be represented by a very narrow lineate groove (sometimes not half the length of the nutlet) or it may be completely fused and obliterated. It may be present or absent or vary in

length not only within the species but also among the nutlets produced by a single plant. The large, nearly circular attachment scar, horizontal or very slightly oblique, is flat or slightly convex and is always distinctly basal. In all species towards its ventral margin the scar bears a prominence composed of the slightly protruding broken end of the well-developed bony tubular funicular canal. In the detached nutlets of *M. viridiflora*, *M. barbigera*, and *M. notata*, the scar also bears another process, this small and obliquely ascending and apparently representing protrudent tissue about the base of one of the vascular traces leading to the dorsum of the nutlet body. This dorsal prominence on the scar appears to be absent on the nutlets of *M. exserta*. Since thoroughly mature, self-detached nutlets of *M. longiflora*, *M. Pringlei*, *M. hispida*, and *M. leonotis* have not been seen, the nature of the scar in these species is unknown. The gynobase in all species is well developed, broadly pyramidal, and terminated by a persisting, more or less thickened four-angulate base of the style. The attachment surfaces of the mature gynobase are usually each encircled by a coarse thickened and elevated cartilaginous margin. When all four nutlets are matured, the gynobase has more or less distinctly sloping attachment faces, and the nutlets they bear, being straight and basifixed, are accordingly divergent.

KEY TO THE SPECIES

Corolla with erect or ascending lobes.
- Back of anthers hairy above the middle; filaments strap-shaped; corolla without glands on the inner surface, villulose in the tube; stigmas terminal on the style ..... 1. *M. viridiflora.*
- Back of anthers glabrous; filaments not strap-shaped; corolla glanduliferous in the throat, tube glabrous inside; stigmas usually subterminal, separated by the sterile tip of the style.
  - Corolla bearing 5 evident cuneiform plaits, these glanduliferous and extending from below the corolla-lobes upward upon the lobes to beyond their middle ..... 2. *M. notata.*
  - Corolla without cuneiform glanduliferous plaits, bearing only inconspicuous small circular or elliptical congregations of glands at or below the base of each corolla-lobe; upper face of lobes glandless.
    - Upper surface of leaves without evident hairs, abundantly and very minutely verrucose or muriculate and hence at most scabrellous; pollen constricted below the middle and bearing the pores above the rounded base ..... 3. *M. longiflora.*
    - Upper surface of leaves bearing evident stiff appressed hairs usually arising from evident pallid dot-like bulbose or discoid bases, surface scabrous; pollen ellipsoidal, broadest at the middle, pores equatorial. 4. *M. Pringlei.*

Corolla with lobes reflexed or (in no. 6) loosely recurved.
- Mouth of corolla densely glanduliferous in a continuous band; stigmas subterminal, separated and surpassed by the short sterile apical prolongation of the style ..... 5. *M. leonotis.*
- Mouth of corolla not conspicuously glanduliferous; stigmas terminal.
  - Corolla-lobes loosely recurved, deltoid, about as long as broad; corolla

regular, symmetric in the bud, stamens all affixed at the same distance above the corolla-base; pollen ellipsoidal, pores equatorial. . . . . 6. *M. barbigera.*

Corolla-lobes becoming reflexed, elongate; corolla zygomorphic, asymmetric in the bud, throat oblique, stamens on adaxial side affixed higher than those on the opposite side of corolla; pollen bearing the row of pores slightly below the middle of the grain.

Filaments 10–15 mm. long; corolla 50–55 mm. long; middle stem leaves usually lanceolate; pollen globose-ovoid . . . . . 7. *M. hispida.*

Filaments 55–70 mm. long, conspicuously long-exserted; corolla very large, 60–90 mm. long; middle stem leaves oblanceolate; pollen ovoid-ellipsoidal . . . . . 8. *M. exserta.*

1. **Macromeria viridiflora** DC. Prodr. **10**: 68 (1846); Sessé & Moc. Calq. Fl. Mex. t. 904 (1874); Johnston, Jour. Arnold Arb. **30**: 110 (1949). Type from Mexico, *Sessé & Mociño.*

Macromeria longiflora sensu Johnston, Contr. Gray Herb. **70**: 14 (1924).

Stems 5–10 dm. tall. Cymes terminal on the stems and frequently geminate and commonly borne also on short leafy branchlets arising from the uppermost axils. Calyx becoming 25 mm. long, largest lobe up to 2.5 mm. broad and the smallest 1–1.5 mm. broad. Corolla greenish yellow, 65–80 (usually 70–75) mm. long, regular or nearly so, outside with abundant appressed and scattered spreading hairs 0.7–2 mm. long, inside sparsely and inconspicuously strigulose along the veins below the lobes and villulose inside the narrow tube, stipitate glands very few or absent, annulus absent or very imperfectly developed. Corolla-lobes triangular-ovate, acute, ascending, 8–10 mm. long, 5–7 mm. broad above the base, usually greenish and sometimes strigose along the middle of the upper surface. Filaments equal, 16–20 mm. long, borne 8–10 mm. below the base of the corolla sinus, broad and strongly compressed, strap-shaped, broadest (ad 1.5 mm.) slightly above the base and then very gradually narrowed towards the apex (ca. 1 mm. wide). Anthers 4–5.5 mm. long, affixed at or slightly below the middle, strictly erect, apex emarginate, base shallowly lobed; connective on upper half of dorsum broad and bearing scattered coarse appressed hairs usually most abundant below the gland at its summit. Pollen elongate, 28–33 × 18–22 μ, somewhat constricted below the middle, bearing the row of pores where broadest 8–10 μ above the base of the grain. Stigmas two, distinctly terminal. Nutlets 3–3.5 mm. long, with an obscure ventral keel, suture absent or represented by a lineate groove.

Mountains of northern Mexico, in the states of Chihuahua and adjacent Durango, Sinaloa, and Sonora, and extending north into the United States only in the mountains (Chiricahua and Huachuca Mts.) of southeastern Arizona.

1a. **Macromeria viridiflora** var. **Thurberi** (Gray), comb. nov.

Onosmodium Thurberi Gray, Synop. Fl. N. Am. **2**[1]: 205 (1878). Type from western New Mexico.

Macromeria Thurberi (Gray) Mack. Bull. Torr. Bot. Cl. **32**: 496 (1905).

Flower smaller than in typical *M. viridiflora*. Calyx becoming 20 mm. long, lobes 1–1.5 mm. broad; corolla 35–50 (usually 40–45) mm. long; filaments 12–14 mm. long, borne 6–8 mm. below the corolla sinus; anthers 3–4.5 mm. long.

Occurring in the mountains from middle eastern New Mexico west to central Arizona in an area to the north of that occupied by typical *M. viridiflora*.

A very well marked species readily recognized by its strap-shaped filaments and dorsally hairy anthers, and also by the villulose inner surface of its corolla-tube.

The typical form of the species has slender, very elongate corollas. Like many other plants of the Sierra Madre Occidental, true *M. viridiflora* has a range that extends north into the Chiricahua and Huachuca mountains, just north of the United States-Mexican boundary, but no further to the northward. Some collections from the Chiricahua and Huachuca mountains are indistinguishable from those of Mexican origin, but others have their flowers somewhat smaller. Even in these latter, however, the corollas are larger than those on plants referable to var. *Thurberi* which occur further northward in New Mexico and central Arizona. The differences in flower size are geographically correlated and sufficiently striking to merit nomenclatorial recognition.

2. **Macromeria notata,** sp. nov.

Planta perennis 4–5 dm. alta e radice valida purpureo-tincta erumpens; caulibus simplicibus foliosis erectis breviter hispidis basim versus ad 5 mm. crassis; foliis numerosis lanceolatis evidenter venosis acutis, eis medium versus caulis gestis majoribus 6–8 cm. longis 16–20 mm. latis, pilos rigidos adscendentis 0.2–1 mm. longos e basi bulboso vel discoideo minuto non rariter pallido erumpentibus proferentibus, facie inferiori pallidioribus venis prominulis ornatis; cyma scorpioidea solitaria caules simplicos terminanti; calyce 15–18 mm. longo, lobis inaequalibus 1–2.5 mm. latis, pedicellis sub anthesi 0–5 mm. longis maturitate 10–15 mm. longis; corolla flavescenti regulariter 50 mm. longa extus hispidula pilis 0.5–1 mm. longis plus minusve curvatis ornata, intus glabra et solum in appendiculis faucium glandulifera; tubo 2–2.5 mm. longo 1–1.5 mm. crasso; annulo anguste annulato; faucibus 1.5–2 cm. longis gradatim ampliatis apicem versus 5–6 mm. crassis; appendiculis faucium depressis elongatis a 2 mm. infra basim loborum corollae sursum fere ad 2 mm. infra apicem loborum corollae prolongatis cuneiformibus leviter invaginatis prominulis dense glanduliferis basi 1–1.5 mm. latis truncatis; lobis corollae triangularibus adscendentibus viridescentibus ca. 5 mm. longis et latis summum ad apicem rotundis secus medium appendiculi faucium glanduliferi decurrenti notatis alibi minute sparseque striguiosis; filamentis 6–9 mm. longis ca. 5–7 mm. infra basim sinuum limbi affixis; antheris 2–2.5 mm. longis rectis apice haud appendiculatis; pollinis ellipsoideis 28–30 × 23–25 μ, poris 8 secus equatorem dispositis; stigmatibus 2, terminalibus; nuculis 4 mm. longis laevibus albis ovoideis obscure asymmetricis obscure carinatis, late basaliter affixis, cicatrice con-

vexo; gynobase subplano, pulvinis distinctis margine cartilagineis prominulis circumdatis.

MEXICO (Nuevo Leon): Ascent of Sierra Infernillo, ca. 15 miles south of Galeana, 9–10,000 ft., common over small areas just below peak, fl. yellow, June 16, 1934, *C. H. & M. T. Mueller 830* (TYPE, Gray Herb.); canyon below Las Canoas on Cerro Potosi, scattered in dense shade on arroyo bank, July 20, 1935, *C. H. Mueller 2238* (G).

The distinctive features of this species are the weakly invaginate elongate densely glanduliferous plaits which extend from the upper part of the throat out upon each of the corolla-lobes. These glanduliferous plaits are the closest approximation in the genus to the localized well-developed faucal appendages present in many species of *Lithospermum*. In *M. longiflora* and *M. Pringlei* there are small vague convex areas bearing glands at or below each lobe of the corolla, but in other congeners of *M. notata*, even this suggestion of faucal invagination is lacking. The present species is certainly a very distinct one. Its closest relations are possibly with *M. Pringlei* and *M. longiflora*.

3. **Macromeria longiflora** [Sessé & Moc.] D. Don, Edinb. New Philos. Jour. **13**: 239 (1832); Johnston, Contr. Gray Herb. **92**: 93 (1930). Type from Mexico, *Sessé & Mociño*.

Lithospermum longiflorum Sessé & Moc. ex D. Don, Edinb. New Philos. Jour. **13**: 239 (1932), in synonym.
Onosmodium longiflorum (Don) Macbr. Contr. Gray Herb. **49**: 21 (1917).
Lithospermum flavum Sessé & Moc. Fl. Mex. 32 (1893): Johnston, Jour. Arnold Arb. **30**: 109 (1949). Type from Michoacan, Mexico, *Sessé & Mociño*.
Macromeria discolor Benth. Pl. Hartw. 49 (1840). Type from Mexico.
Onosmodium discolor (Benth.) Macbr. Contr. Gray Herb. **49**: 20 (1917).

Cymes terminal on the stems and frequently also arising directly from the uppermost axils. Calyx 13–15 mm. long, lobes slender, 1–1.5 mm. broad, unequal. Corolla 45–55 mm. long, regular or very obscurely prolonged on the adaxial side, outside clothed with slender spreading or loosely appressed hairs up to 1 mm. long, inside bearing inconspicuous elliptic congregations of glands on obscurely convex areas below each corolla-lobe and sometimes glands also along the decurrent base of the filaments, annulus not developed. Corolla-lobes elongate, lance-oblong, acutish or the tips obtusish, 11–15 mm. long, 4–7 mm. broad, ascending, upper face without hairs or glands. Filaments 14–15 mm. long, affixed ca. 4 mm. below limb-sinus, anthers 2–4 mm. long, affixed at or near the middle, erect, apex minutely appendaged. Pollen elongate, 25–28 × 16–18 μ, constricted below the middle, broadest and bearing the row of pores about 8 μ above the base. Stigmas 2, usually subterminal. Nutlets ovoid, erect, symmetric, 4 mm. tall, 3 mm. thick.

Mountains of western Mexico from Colima to Oaxaca.

A species probably most closely allied to *M. Pringlei*, from which it differs in its more herbaceous stems and its larger leaves devoid of evident

hairs on the upper surface. Although at first glance the upper leaf face appears to be smooth and glabrous, close examination under the microscope shows it to be actually dotted with minute mineralized warts or conic muriculations. When the minute roughenings are pointed, the surface may be perceptibly scabrellous. The minute mineralized roughenings on the leaf of *M. longiflora* are evidently homologous with the very much coarser bulbose or discoid hair bases present on the upper leaf face of *M. Pringlei*. The lower face of the leaves in *M. longiflora* is strigose with an abundance of short, stiff, closely appressed hairs. It is usually cinereous and contrasts very strongly with the upper surface, which in most herbarium specimens dries a chocolate brown.

4. **Macromeria Pringlei** Greenm. Proc. Am. Acad. **34**: 570 (1899). Type, Sierra de Pachuca, Hidalgo, *Pringle 11044*.

Onosmodium Pringlei (Greenm.) Macbr. Contr. Gray Herb. **49**: 20 (1917). *Macromeria guatemalense* Johnston, Jour. Arnold Arb. **29**: 232 (1948). Type, Volcán Tajumulco, dept. of San Marcos, Guatemala, *Steyermark 35898*.

Cymes terminal on the stems and frequently also terminating short axillary branches arising from the uppermost axils. Calyx 12–15 mm. long, lobes slender, 0.5–1.2 mm. wide. Corolla pale yellow-green, 35–53 mm. long, regular, straight, outer surface bearing slender ascending hairs ca. 1 mm. long, inside glabrous bearing very scattered glands, or these only in very vague slightly swollen areas at or below the base of the corolla-lobes. Corolla-lobes triangular, acute, erect or ascending, 9–10 mm. long, 5.5–7.5 mm. broad, apex obtusish, upper face usually without hairs or glands. Filaments 9–12 mm. long, equal, affixed in the throat 3–4 mm. below the base of the corolla sinus. Anthers 2–3.5 mm. long, medio-affixed, apex minutely appendaged. Pollen ellipsoidal, sides rounded or nearly parallel, 25–26 $\times$ 15–18 μ. Stigmas 2, subterminal. Nutlets erect, symmetric, pointed, ca. 4 mm. tall, 3–3.5 mm. thick, without a ventral keel.

Mountains of Mexico in the states of Hidalgo, Guerrero, and Oaxaca.

Closely related to *M. longiflora* but a less vigorous plant with more slender fruticulose stems and smaller, usually more elongate leaves bearing evident appressed hairs on the upper surface. *Macromeria guatemalense* of northern Guatemala appears to differ from Mexican *M. Pringlei* only in its more elongate, more decidedly fruticose stems and smaller (to 35 mm. long) corollas. Possibly it may represent a southern variety of *M. Pringlei*, but hardly a species distinct from it.

5. **Macromeria leonotis** Johnston, Jour. Arnold Arb. 16: 188 (1935). Type, ascent into Taray, Sierra Madre ca. 15 mi. s.w. of Galeana, Nuevo Leon, *Mueller 754*.

Cymes terminal on the stem. Calyx 19–25 mm. long, lobes unequal, very slender, 1–1.5 mm. wide. Corolla yellow, 55–75 mm. long, slightly zygomorphic, straight or somewhat curved, outside hispidulose-villulose, densely clad with short curly hairs 0.3–0.7 mm. long, inside glanduliferous on the

lower part of the lobes and over the upper half of the throat and most abundantly so in a band at the throat summit; annulus a very narrow interrupted ring bearing five groups of short, very inconspicuous hairs. Corolla-lobes triangular-oblong, 7–12 mm. long, 5–8 mm. wide, becoming reflexed, apex rounded, upper surface minutely strigulose or rarely glabrous, glanduliferous at the base. Filaments 14–20 mm. long, compressed, affixed 7–8 mm. below the corolla sinus, sometimes hairy below the middle and on the decurrent base. Anthers 2–3.5 mm. long, affixed just below the middle, apex minutely appendaged. Pollen broadly globose-ellipsoidal, sides angulate, 25–26 × 23 μ, pores 8, equatorial. Stigmas apparently subterminal. Nutlets not seen.

Mountains of northeastern Mexico in states of Nuevo Leon and Tamaulipas.

A species notable for its short soft indument and abundantly glanduliferous summit of the corolla-throat. The corolla appears to be slightly zygomorphic, being somewhat curved and perhaps also slightly prolonged on the adaxial side. The elongate lobes are strongly reflexed at the base and the opening into the throat is accordingly the most forward part of the corolla. The rounded lip surrounding this opening to the throat is densely glanduliferous. Some glands are present on the lower part of the corolla-lobes and also inside the throat down at least to the level of the stamen attachments, but only on the lip about the opening into the throat are they extremely abundant. No other species of the genus has corollas with glands so numerous. The species is a very distinct one, but seems to share more characters with *M. longiflora* and *M. Pringlei* than with other congeners.

6. **Macromeria barbigera** Johnston, Jour. Arnold Arb. 16: 189 (1935). Type, slope of Sierra Tronconal, ca. 15 mi. s.w. of Galeana, Nuevo Leon, *Mueller 741*.

Cymes terminal on the stem and also arising from the uppermost leaf axils. Calyx 15–20 mm. long, lobes very slender, 1–1.5 mm. broad, unequal. Corolla ("cream-white" but when dry with a distinctly reddish throat and somewhat greenish lobes) 45–65 mm. long, regular, with a very slender tube 15–30 mm. long which abruptly expands into a cylindric throat that is 20–30 mm. long, 5–10 mm. thick, and sometimes perceptibly broadest below the middle, outer surface of corolla villose, the hairs slender, white, and 2–3 mm. long, inner surface glanduliferous above the level of the filament attachments and especially so on the upper face of the lobes, annulus an interrupted ring. Corolla-lobes deltoid, 4–5 mm. long, loosely but distinctly recurved especially beyond the middle. Filaments 12–15 mm. long, affixed 8–10 mm. below the base of the corolla sinus. Anthers 2–3 mm. long, medio-affixed, apex minutely appendaged. Pollen ellipsoidal, sides rounded or angled, 30–33 × 25–28 μ, pores 9, equatorial. Stigmas terminal. Nutlets ellipsoidal to ovoid, 3–3.5 mm. long.

Northeastern Mexico in the mountains of Nuevo Leon and Tamaulipas.

A very distinct species notable for its coarse habit, bristly indument, and

broad leaves, as well as for the form of its large corollas. The corollas have a very slender tube, an abruptly expanded elongate throat, and loosely recurved deltoid lobes glanduliferous on the upper surface. The immediate relatives of the species are obscure.

7. **Macromeria hispida** Mart. & Gal. Bull. Acad. Brux. 11: 339 (1844). Type, near Morelia, Michoacan, *Galeotti 1917*.

Macromeria longiflora var. *hispida* (M. & G.) A. DC. Prodr. **10:** 68 (1846).
Onosmodium longiflorum var. *hispidum* (M. & G.) Macbr. Contr. Gray Herb. **49:** 21 (1917).
Macromeria longiflora sensu DC. Prodr. **10:** 68 (1846).

Cymes terminal and commonly also arising directly from a number of the uppermost axils to form an elongate thyrse. Calyx with very unequal lobes, the abaxial one largest and becoming 18–22 mm. long and 1.5–2.5 mm. broad. Corolla yellow, 50–55 mm. long, zygomorphic, usually somewhat curved and the throat prolonged on the adaxial side, in the bud thickly clavate with the outer half swollen and evidently more rounded on the adaxial side, outer surface of corolla bearing numerous ascending or loosely appressed hairs 0.5–1 mm. long, inside bearing scattered inconspicuous slender gland-tipped hairs in the throat above the stamen attachments and also on the upper face of the lobes; annulus not developed. Corolla-lobes equal, elongate, ovate-elliptic, 8–10 mm. long, 6–7 mm. broad below the middle, becoming reflexed, apex rounded, margins revolute. Filaments equal, 10–15 mm. long, affixed at slightly unequal heights above the corolla base, the medial adaxial filament ca. 2 mm. higher than the abaxial pair and ca. 1 mm. above the adaxial pair, all attached 4–5 mm. below the oblique summit of the throat. Anthers 2–3 mm. long, affixed slightly below the middle, erect, apex frequently bearing a slender minute appendage. Pollen globose-ovoid, 38–41 $\times$ 33–37 μ, upper and lower halves of the grain slightly unequal, pores eight in a row and borne slightly below the middle. Stigma terminal. Nutlets not seen.

A Mexican plant known only from the state of Michoacan, especially near Morelia and Patzcuaro.

In floral organization this species most resembles *M. exserta*, but in general habit it is more suggestive of *M. Pringlei* and *M. longiflora*.

8. **Macromeria exserta** D. Don, Edinb. New Philos. Jour. 13: 239 (1832); Lindley, Bot. Reg. 33: t. 26 (1847). Type from Mexico, *Sessé & Mociño*.

Echium longiflorum Sessé & Moc. Pl. N. Hisp. 20 (1888); Johnston, Jour. Arnold Arb. **30:** 109 (1949).
Macromeria exserta var. *imparata* Macbr. Contr. Gray Herb. **49:** 22 (1917). Type from Oaxaca, 1842, *Ghiesbreght*.

Cymes terminal and commonly also arising from the uppermost axils to form a loose thyrse. Calyx 20–30 mm. long, lobes very unequal, 1–7 mm. broad. Corolla very large, 60–90 mm. long, yellow, zygomorphic, with the

tube curved and the throat prolonged on the adaxial side, in the bud with its thickened distal half conspicuously distended on the adaxial side, outside of corolla bearing abundant spreading hairs usually ca. 0.5 mm. long, inner surface of throat and lobes bearing scattered, usually inconspicuous slender gland-tipped hairs; annulus not developed. Corolla-lobes elongate, equal, 15–28 mm. long, 5–8 mm. broad, becoming reflexed, apex rounded or obtusish, margins revolute. Filaments very slender, elongate and long-exserted, 55–70 mm. long, usually curved, affixed in the corolla-throat 4–5 mm. below its oblique summit at three superimposed levels, the odd medial stamen 5–8 mm. higher above the corolla base than the abaxial pair and 3–4 mm. above the adaxial pair. Anthers 3–4 mm. long, frequently curved, affixed below the middle, becoming versatile, apex usually bearing a minute appendage. Pollen ovoid-ellipsoidal, 38–41 × 25–28 μ, upper and lower halves of grain slightly dissimilar, pores 8, slightly inframedial. Stigmas terminal. Nutlets 4–5.5 mm. long, 2.5–4.5 mm. thick, weakly keeled.

Mountains of western Mexico from Nayarit to Oaxaca.

A very distinct species notable for its very coarse habit and extremely large zygomorphic corollas with excessively long-exserted stamens. Because of the curved adaxially swollen buds and the eventually long-exserted curved stamens the corolla has a form and appearance more suggestive of some of the Verbenaceae, e.g., *Clerodendron*, than of other members of the Boraginaceae. In size the corolla of *M. exserta* surpasses that of all other species in the whole of the Boraginaceae.

2. **Onosmodium** Michx. Fl. Bor. Am. 1: 132, t. 15 (1803). Based upon *O. hispidum* Michx. [= *O. virginicum* L.] and *O. molle* Michx.

Osmodium Raf. Med. Repos. N. Y. 5: 353 (1808); Merrill, Index Raf. 203 (1949). A substitute name for *Onosmodium* Michx.

Purshia Spreng. Anleit. ed. 2, 2: 450 (1817); Lehm., Asperif. 2: 382 (1818). A substitute name for *Onosmodium* Michx.

Osmidium Walp. Ann. 3: 134 (1853). Apparently a printers' mistake for *Onosmodium* Michx.

Plants perennial, with few to many frequently coarse, erect stems, strigose or more commonly hispid, glanduliferous in one species only, simple or bearing ascending leafy fertile branches above the middle. Leaves mostly cauline, numerous, bearing several pairs of strong assurgent veins; lowest leaves usually larger and more elongate than the middle and upper ones, usually shed before the time of flowering, persisting in only a few species. Cymes scorpioid, single or paired, borne terminal on the main stem and its branches, usually many-flowered, at first dense and coiled and later in the fruiting condition becoming straight, greatly elongate, and loosely flowered. Bracts numerous, one adjacent to each flower, lanceolate to ovate, becoming large and conspicuous in age, foliaceous. Calyx 5-fid; lobes attenuate or broadly linear or slightly spathulate, acute to obtuse or rounded at the apex, usually evidently unequal, after maturity of the

fruit usually disarticulating at the base. Pedicels short to elongate. Corolla opening (and its style exserted and its anthers mature) while incompletely developed. Mature completely developed corolla white to cream or yellow, usually with the lobes more or less green or greenish, subtubular, two to three times as long as broad, regular, straight; outside hairy, usually strigose or with appressed hairs; inside glabrous (or a few hairs near the tip of the lobes in one species), without any glands or true faucal appendages; annulus evident, consisting of a narrow flange or ten lobules, glabrous; throat usually about twice the thickness of the corolla-base, broadest (and in lateral silhouette somewhat angulate) a short distance below its summit, bearing ten externally protrudent gibbose convexities, five below the base of the corolla-sinus and five lesser ones below the corolla-lobes. Corolla-lobes nearly one half to nearly one fifth (but most commonly about one third) the total length of the corolla, erect, more or less elongate, very narrowly imbricate in the bud, cuneate or triangular or ovate-triangular with the apex acute or acute with an attenuate tip; sinus between the lobes narrow, acute, thickened and inflexed at the very base. Stamens borne at equal heights in the thickest part of the throat, affixed at or distinctly above the middle of the corolla; filaments short, usually somewhat unguiculate, one third the length of the anthers or less; anthers oblong-lanceolate, with their tips reaching up to or slightly beyond the base of the corolla-sinus, affixed between the base and the middle usually at about one third of its total length above its base; apex of anther bearing a minute appendage (appendage semicircular or quadrate or three-lobed or sometimes attenuate, composed of prolongations of the thecae and the narrow connective, with the portion prolonged from the connective frequently darkened and perhaps glandular); base of anther emarginate or lobed, reaching downward in the corolla-throat to or distinctly below the point of attachment of the filaments; connective narrow, glabrous; thecae below the anther attachment distinct and usually spreading, their basal tips very obscurely if at all thickened. Pollen small, 16–24 $\times$ 13–22 μ, ovoid to globose-ovoid, lower half rounded more broadly and evenly than the upper half, always longer than broad, though at times only slightly so; pores inframedial, six or seven in a single row, usually obscure; grains in polar profile circular or rarely somewhat polygonal. Style filiform, precociously long-exserted, emerging from the incompletely developed corolla when the latter has not yet attained half of its eventual size; stigmas two, minute, terminal on the style. Ovules four but usually only one maturing and very rarely more than two. Nutlets ovoid or ellipsoidal, white or tawny, lustrous, smooth or pitted, gradually narrowed to the base or sometimes with a suprabasal constriction, nearly circular in transverse section, lacking a prominent ventral keel or any evidence of a ventral suture; attachment-scar flat, basal, nearly as broad as long, towards ventral edge bearing the slightly prominent broken end of the bony tubular funicular canal and towards the dorsal edge a small, attenuate, obliquely ascending prominence representing a thickening of scar tissue about the base of a vascular strand leading to the dorsum of the nutlet body. Gynobase de-

pressed, nearly flat, attachment surface plane, distinct, lacking strongly thickened upturned margins.

A genus confined to middle and eastern sections of the United States and to northeastern Mexico. Most authors have recognized seven species within the United States, cf. Mackenzie, Bull. Torr. Bot. Cl. 32: 495–506 (1905); Johnston, Contr. Gray Herb. 70: 17–18 (1924); and Fernald, Manual Bot. 1200–1201 (1951). Two additional species are endemic to northeastern Mexico. Of the total only four are sharply definable and always positively recognizable, viz., *O. unicum* Macbr. and *O. dodrantale* Johnston of Mexico, *O. Helleri* Small of Texas, and *O. virginianum* (L.) DC. of the eastern border of the United States. The other five "species" intergrade and are incapable of sharp definition. There is *O. hispidissimum* Mack., ranging in the Ohio Valley and the Middle Atlantic States, *O. occidentale* Mack., widespread in the region between the Mississippi River and the Rocky Mountains, and *O. bejariense* DC., confined to Texas. These three are habitally similar and obviously related, and over the larger portion of the area in which they are found they seem relatively constant in their characters. Another group of related plants is practically confined to Tennessee, Kentucky, Arkansas and Missouri. These have slender stems and an indument usually closely appressed and frequently scanty. Representative of them are *O. molle* Michx. and *O. subsetosum* Mack. Embarrassing transitional forms between these two groups, as well as between their members, appear to be frequent in Missouri, Iowa, and Illinois, where the ranges of the various species converge or even overlap. Analysis will probably reveal evidence of much hybridization and intragression affecting *O. hispidissimum*, *O. occidentale*, and *O. molle* in that area.

The genus has general relations with *Macromeria* and *Lasiarrhenum* but is more closely related to the American and particularly to the Mexican species of *Lithospermum* and, along with the two genera mentioned, is probably derived from them. It is a sharply defined and thoroughly natural group readily recognizable by a number of strong characters. Particularly noteworthy are its precociously sexual flowers. In these the anthers mature and the style becomes long exserted in corollas that have opened before they have attained half their eventual size. The subtubular corolla is also distinctive in having very narrowly imbricate, erect, sharply acute or acuminate corolla-lobes and sinuses between the lobes which are distinctively thickened and inflexed at the very base. The corolla-throat may have five to ten gibbose swellings outside, but inside is devoid not only of faucal appendages but also of any hairs or glands. The included glabrous anthers are attached between base and middle to very abbreviated filaments and are appendiculate at the apex and lobulate at the base.

Most of the species commonly referred to *Onosmodium* are obviously congeneric. To be excluded, however, are *O. revolutum* (Robins.) Macbr., Contr. Gray Herb. 49: 21 (1917), the type of the genus *Psilolaemus*, and *Onosmodium strigosum* (HBK.) Don, the type of the genus *Lasiarrhenum*. Gray, Synop. Fl. Am. 2[1]: 205 (1878), and later Macbride, Contr. Gray

Herb. 49: 19 (1917), have suggested that all species of *Macromeria* except *M. exserta* should be accommodated in an enlarged *Onosmodium*. Justification for this apparently rests solely on general vegetative similarities and in the fact that corolla-lobes of *Macromeria* may be acute. In size, form, and behavior of the corolla and in structures inside the corolla the species of *Onosmodium* are extremely different from those of *Macromeria*. Indeed, the two genera differ more from each other than they do individually from *Lithospermum*. If generic values are not to be lowered, *Onosmodium* and *Macromeria* must be kept distinct.

In the Mexican *O. dodrantale*, the plant not only has very short stems, 1–3 dm. long, but also has the leaves smallest at the base of the stem and gradually increasing in size upward along it. In the other species of the genus, all of them with much longer stems (usually 5–12 dm.), the leaves at the base of the stem are larger and more elongate than those on its middle sections. The indications are that the stems elongate from the center of a winter rosette of leaves and not directly from a bud on the caudex, as in *O. dodrantale* and in most species of *Lithospermum*. The large lowermost leaves have usually fallen away in herbarium specimens of most species. Indeed, only in those of *O. bejariense* and *O. Helleri* are they commonly found dried up and still persisting in some numbers crowded at the base of the stem. In most species the foliage has reached full size and has become firm before anthesis. This is not the case, however, in *O. Helleri*. In that species the plant flowers while it is still growing vigorously and before it has attained full stature and the upper leaves have attained their maximum size and mature firmness. Plants of *O. Helleri* at anthesis and those maturing fruit have a very different appearance. In fruiting plants of this species the bracts become unusually large and conspicuous.

The cymes in *O. dodrantale* are weakly developed and hardly more than three- to six-flowered bracteate glomerules terminating the short stems. In the other species of the genus, however, they are distinctly scorpioid and abundantly flowered and eventually become straight, extremely elongate, and very loose at extreme maturity. The flowers maturing their corollas are borne crowded on the arched summit of the cyme, those with completely grown corollas just above the point where the rachis begins to straighten. Since the pedicels are strict, the corollas incline backwards towards the summit of the cyme, and those near its summit become nearly horizontal. After the corolla is shed the rachis straightens, its internodes elongate, and the abundant bracts, previously inconspicuous, increase in size and become very conspicuous.

The indument on the herbage may be either strigose or bristly. *Onosmodium subsetosum* is unusual in having the stems glabrous or nearly so. A very distinctive feature of the Mexican *O. unicum* is the presence of very slender multicellular, gland-tipped hairs intermixed among the stiff ascending hairs on the leaves, stems and rachis of the cyme and even on the calyx. I know of no other American herbaceous borage having generally distributed hairs of this type.

The flowers of *Onosmodium* are precociously sexual. The corolla opens and its anthers are matured and its style is exserted long before the corolla has attained full size, commonly when it is less than half its eventual size or even sufficiently elongate to surpass the calyx. In this behavior of the corolla the genus differs from all other American Boraginaceae, and among the Lithospermeae, at least, has a parallel only in the monotypic *Halacsya* of Albania and Montenegro, cf. Jour. Arnold Arb. 34: 276 (1953). On the densely flowered arched summit of the scorpioid cyme in *Onosmodium*, as in *Halacsya*, the styles are to be seen projecting not merely from the fully developed conspicuous corollas but also above the latter from a series of gradually less well developed corollas on younger and higher parts of the cyme. The style may first emerge when the corolla is so small as to be overtopped by its calyx lobes. When the corolla is sufficiently large to equal or slightly surpass the calyx, the style is long exserted, the corolla-lobes have unfolded completely, and the anthers have attained nearly full size and in herbarium specimens are dehiscent. At this stage, above the level of the filament attachments the corolla is approaching mature form and has attained about seventy-five per cent of its eventual size. Below the level of the filament attachments, however, growth has lagged, for the tube is still very short and scarcely developed. It is after the corolla opens and the anthers and style are exposed and functioning that the tube elongates and increases in diameter and the corolla achieves full size and mature proportions. The early emergent, eventually long exserted style evidently makes self-pollination in this genus practically impossible. How the corolla may function in pollination during the period in which it doubles its size after opening and maturing its anthers is a subject deserving investigation.

The fully developed corolla in this genus may be 8–12 mm. long, as in *O. virginianum* and *O. hispidissimum*, or as much as 12–18 mm., as in *O. occidentale*. From a base 1.5–2.5 mm. thick they gradually expand upwards to just below the summit of the tube where they are broadest, ca. 4 mm. in *O. virginianum* and 6–7 mm. in most other species. The lobes are a third to a fifth (usually about a third) the total length of the corolla. They are cuneate to triangular or ovate-triangular, and from the base or just above it contract with straight convergent sides to the sharp apex, which is acute or sometimes (in *O. unicum*) acute with an attenuate tip. The lobes, except near the very margin (i.e., on all surfaces exposed while folded in the bud), have their outer face hairy, as elsewhere on the outside of the corolla. The inner face of the lobes is usually completely glabrous. Indeed, the only exception is in the corolla of *O. dodrantale*, which is unique in having the inner surface of its lobes always inconspicuously hairy just below their tip. In the bud the lobes are imbricate very narrowly and only sufficiently to produce a very narrow glabrous margin, narrowing upward, on the dorsum of each lobe. It is this very narrow imbrication of the lobes, becoming negligible towards the tip of the bud, that facilitates the early egress of the precociously elongating style that has pushed upwards inside the very immature flower bud.

The base of the acute sinus between the erect corolla-lobes is distinctly plicate, inflexed, and thickened. A somewhat similar condition occurs in the flowers of some species of *Heliotropium*, but among the Lithospermeae in no other genus save *Onosmodium* is it present or at least so well developed. In most species the corolla is locally distended outwardly by convex gibbose swellings, one directly below the plicate base of each sinus. These gibbosities make the corolla more or less five-angled just below the summit of the throat where it is broadest. Gibbosities of a similar sort may also be present below the base of each corolla-lobe and alternate with those below the sinus, but are usually less conspicuous than the latter. Inside the corolla-throat, except for the inflexed bases of the sinus, there are no intrusive appendages or invaginations. Faucal appendages and stipitate glands, common features in the corolla-throat of other Lithospermeae, are completely absent. Pubescence of any sort is also absent inside the corolla, even on the annulus. The annulus is clearly developed, either as a narrow thickish continuous flange or as ten lobes.

The anthers, 2.5–3.5 mm. long, are attached to a very short filament at about a third of their length above their base, and hence very definitely below their middle. The filaments, a third the length of the anther or less, are attached in the corolla commonly about 2 mm. below the summit of the throat. The anthers, accordingly, usually reach up to about the base of the sinus above them or at most have their tips only a millimeter beyond. The base of the anther projects downward to the same level as the attachment of the filament on the walls of the throat or slightly below it. In the lower quarter of the anther the thecae are not united. They may remain parallel and the base of the anther appear emarginate, but usually, particularly in age, they tend to spread, making the anther lobulate at the base. The thecae are only slightly narrowed above the middle. The anther is always minutely appendiculate at the apex. The very diminutive appendages appear to be formed not merely by a prolongation of the narrow connective but also by apical prolongations of each theca. These parts may be confluent or distinct. The appendage is variable in form within the species, and even according to the age of the anther bearing it. It may be three-pronged, it may be quadrate with either truncate or toothed summit, or occasionally, in *O. dodrantale* and *O. unicum*, subulate or lanceolate. In *O. virginianum* the anther summit may be even broadly emarginate and the thecae each tipped by a minute appendage and distinct from the third small appendage arising from the depth of the sinus between them.

The pollen of the various species of *Onosmodium* differs slightly in size but very little in shape. It is ovoid, or at times, even in the same species, very broadly so and even globose-ovoid in form. The grains are always perceptibly longer than broad with the upper and lower half differing to some degree in outline. In lateral profile the pores are at most very weakly protrudent. Usually they are very obscure. They are borne in a single row perceptibly below the middle of the grain and are usually six but not infrequently seven in number. In polar profile the grains are

almost invariably circular in outline. The size of the grain seems to be roughly correlated with corolla-size. Species with large flowers usually have grains larger than those in species with small flowers. Small-flowered *O. virginianum* produces the smallest pollen, 15–18 × 13–16 μ. In *O. subsetosum*, *O. molle*, *O. hispidissimum*, and *O. Helleri* the grains measure 16–18 × 15–16 μ, in *O. unicum*, 16–22 × 15–18 μ, in *O. occidentale*, 18–22 × 16–20 μ, in *O. bejariense*, 20–22 × 16–20 μ, and in *O. dodrantale*, 22–24 × 20–27 μ.

As in the case of all genera of the Lithospermeae previously examined, pollen production in *Onosmodium* was found to be prevailingly normal and abundant, with imperfect pollen very scanty and infertile anthers rare. Worthy of note, therefore, is the fact that the reverse condition seems prevalent in *O. occidentale* over the northern parts of its range, in the northern Plains and adjacent Rockies. The species deserves cytological examination.

The nutlets of the genus are generally similar to those of *Lithospermum*. Unlike those of *Macromeria* their ventral suture is always closed and completely obliterated. There is no appreciable ventral keel. Although the ovary is four-ovulate, flowers of the genus seldom mature more than a single nutlet. Only in *O. occidentale* are the exceptional fruits, frequently present in limited numbers, found to be maturing two nutlets. In that species fruit with three nutlets may be encountered very rarely, but none with four nutlets have been found. Accordingly I have not seen a symmetrically developed gynobase. In those maturing one to three nutlets, the attachment faces are nearly horizontal and plane or nearly so. The faces are not concave, nor do they have strongly thickened upturned margins as in *Macromeria*. The attachment scar on the nutlet is flat, not convex as in *Macromeria*, but, like the scar in that genus, it does bear a projecting end of the broken tubular funicular canal, and also another more dorsal projection in the form of an obliquely ascending protuberance.

3. **Nomosa**, gen. nov. Lithospermeae.

Planta perennis herbacea strigosa. Caules hornotini erecti simplices foliosi ut videtur e caudice ex caulibus vetustis 3–4 mm. crassis procumbentibus laxe ramosis composito orientes. Folia breviter strigosa cinerea vel plus minusve argentacea supra basim triplinervia. Folia basalia oblanceolata in fasciculos steriles aggregata. Folia caulina numerosa sessilia a basi caulis sursum gradatim majora, superiora anguste oblonga vel lanceolato-oblonga apice acuta vel plus minusve obtusa. Cymae terminales geminatae laxe scorpioideae pauciflorae tandem rectae racemosae. Bracteae numerosae foliaceae haud conspicuae calycem haud superantes. Flores sub anthesi in parte curvato supremo symae gesti erecti vel horizontales vel declinati. Calyx 5-fidus; lobis evidenter inaequalibus firmis costatis elongatis linearibus vel cuneatis. Pedicelli crassiusculi stricti modice elongati. Corolla ut videtur alba regularis crasse tubularis, calyce subduplo longior, a basi sursum lente gradatimque ampliata (haud faucibus distinctis donata) in tertia parte superiore crassissima, triplo longior quam lata, extus dense brev-

iterque strigosa, intus inter basis decurrentis filamentorum pilis gracilibus glanduliferis praedita alibi glabra; faucibus nec appendiculas nec glandulas stipitatas proferentibus; lobis imbricatis parvis quam longitudine corollae 10-plo brevioribus erectis late ovatis infra medium latissimis basi aliquantum contractis tam longis quam latis vel paullo latioribus quam longis; annulo nullo. Filamenta angusta elongata sursum gradatim attenuata crassiuscula, in quarta parte inferiore corollae affixa, supra medium teretia et glabra, infra medium plus minusve compressa et pilis gracilibus glanduliferis abundanter donata, basi breviter decurrentia incrassata pilis glanduliferis vestita. Antherae elongatae lanceolatae, supra basim affixae, filamentis duplo breviores, in parte suprema tubi corollae gestae, basim versus latissimae deinde sursum gradatim angustatae, appendiculis sterilibus pallidis gradatim attenuatis e tubo corollae exsertis sed lobos corollae haud superantibus terminatae, dorso connectivum pallidum laeve latum (latitudine quam antheram triplo angustius) pilis paucis (1–4) rigidis valde adpressis praeditum proferentes; thecis basim versus distinctis sed parallelis infra medium apicem versus angustatis, basi imo acutiusculis apiculo inconspicuo incrassato donatis sed nullo modo appendiculatis. Granulae pollinis late ovoideae 25–28 × 21–23 μ infra medium latissimae et ibi 7 vel 8 poris obscuris instructae, a latere visae late ovatae ca. 8 mm. supra basim semicircularem latiores deinde sursum per margines rectos convergentes in apicem latum abrupte rotundum contractae. Stylus gracilis glaber tandem evidenter exsertus; stigmatibus 2 distinctis terminalibus. Nuculae ignotae. — Nomen a *Onosma* litteris interversis desumptum.

Nomosa Rosei, sp. nov.

Planta 25–30 cm. alta; caulibus erectis basim versus ad 3 mm. crassis pilis rectis antrorsis laxe adpressis ad 1 mm. longis vestitis, internodiis brevibus ca. 5 mm. longis; foliis strigosis (pilis valde adpressis rectis 0.2–0.6 mm. longis), margine inconspicue ciliolatis (pilis strictis vel adscendentibus 0.5–1 mm. longis), costa 10–20 mm. supra basim nervos 2 assurgentes validos conspicuos perelongatos proferenti donatis; foliis basalibus 40–60 mm. longis supra medium 8–12 mm. latis; foliis caulinis superioribus 40–55 mm. longis medium versus 8–10 mm. latis; cymis ca. 10-floris maturitate rectis ad 8 cm. longis; lobis calycis strigosis margine hispido-ciliatis, sub anthesi 8–11 mm. longis tandem 10–15 mm. longis, lobo majore 1–3 mm. lato quam lobis minoribus 3–5 mm. longiore; pedicello sub anthesi 3–5 mm. longo tandem ad 8 mm. longo recto; corolla 20 mm. longa a basi 2–3 mm. crasso sursum gradatim expansa, 5 mm. infra basim loborum 7 mm. crassa, apice (basi ima loborum) ca. 6.5 mm. crassa; lobis corollae 2 mm. longis medium versus 2–2.5 mm. latis, basi ima 2 mm. latis; filamentis 9.5–10 mm. longis, 5 mm. supra basim corollae orientibus, basim versus 1 mm. latis, apicem versus ad 0.5 mm. latis, infra medium pilos 0.5 mm. longos proferentibus; basi decurrente filamenti incrassato 2–3 mm. longo ca. 0.8 mm. lato pilis glanduliferis vestito; antheris 5 mm. longis ca. 1.4 mm. supra basim affixis, thecis 3.5 mm.

longis basi 3–3.5 mm. infra basim loborum corollae gestis; appendiculo terminali antherae 1.5 mm. longo imam ad basim ca. 0.5 mm. lato; stylo 23–25 mm. longo.

MEXICO: in Sierra Madre near the southern border of the state of Durango, Aug 16, 1897, *J. N. Rose 2360* (TYPE, Gray Herb.).

This remarkable plant is known only from a collection made over a half-century ago by J. N. Rose during his first expedition to Mexico. In general appearance it mimics *Onosma* to a remarkable degree. The original collection was distributed with locality data given merely as "Durango." Accepted as a member of the large and diverse Old World genus *Onosma*, and believed to have been introduced into Mexico, presumably at Durango City, the plant attracted no careful study, particularly since no plant similar to it was subsequently found in America. Only recently, when it was dissected and carefully compared during a study of *Onosma* and related genera, were the very many distinctive features of this neglected Mexican plant fully recognized. Upon investigation it was found that the specimens were made not at Durango City, but rather in the Sierra Madre, ca. lat. 22° 15′ N., at the extreme southern end of the state of Durango, in a wild and infrequented area. It was discovered by Rose when on horseback and with pack-animals he journeyed through Nayarit across the southern tip of Durango and on eastward into Zacatecas, crossing the Sierra Madre in a section not subsequently visited by a botanist. Our plant is apparently endemic in the mountains of this particular region.

Although extremely suggestive of *Onosma* in external features, *Nomosa* is actually a very close ally of the Mexican *Lasiarrhenum*. Its affinities are with such American genera as *Lasiarrhenum*, *Macromeria*, and *Onosmodium*, which appear to be derivatives of American *Lithospermum* rather than of the strictly Old World *Onosma*. Along with *Lasiarrhenum*, *Nomosa* is distinguished from *Onosma* by its 7–8-porate pollen, unequal calyx-lobes, triple-nerved leaves, and free anthers with hairy connectives. From *Lasiarrhenum* it differs in having very elongate gradually narrowed filaments which are attached very low in the corolla and, below the middle, are densely clothed with an abundance of slender elongate multicellular gland-tipped hairs. The anthers, only half as long as the filaments, are carried higher in the corolla and have their elongate terminal appendage exserted from the mouth of the corolla. Unlike the anthers of *Lasiarrhenum*, which are abundantly and conspicuously hairy on the back, those of *Nomosa* bear only a very few closely appressed, much shorter inconspicuous hairs on the connective. The corolla of *Nomosa*, coarsely tubular, does not swell into a campanulate throat as in *Lasiarrhenum*. Its lobes are ovate rather than deltoid, and the inner surface of the throat bears no hairs nor stiped glands. The annulus, very well developed in *Lasiarrhenum*, in *Nomosa* is absent or obscure.

The plant is not bristly. The foliage is closely strigose with the minute hairs abundant but not extremely crowded nor overlapping. The thin indument is tidy and smooth and gray or somewhat silvery. The leaves

usually have only two strong elongate veins. These arise from the midrib 1–2 cm. above the leaf-base. They are assurgent and nearly as strong as the midrib and are frequently prolonged almost to the leaf-tip. Occasionally less well developed veins may also be present, but these are never as conspicuous as the major veins. The corolla, if not perfectly regular, departs from that condition only by having its two adaxial lobes perhaps very slightly larger than the other three. The lobes are involutely curved, and the upper half of the tube directly below each of them is somewhat swollen. The upper half of the corolla, accordingly, has five weakly inflated ribs. The filaments are attached unusually low in the corolla. The position of their thickened short decurrent base is marked on the outside of the corolla by five oblong-elliptic glabrous areas extending 2.5–5 mm. above the corolla-base. The slender, elongate, gradually narrowed filaments are glabrous above the middle, but below the middle and on their thickened decurrent base they bear multicellular gland-tipped hairs in great abundance. This shaggy indument on the filaments is a distinctive feature of *Nomosa*. Some of the multicellular gland-tipped hairs occur also on the walls of the corolla immediately adjacent to the stamen bases. Elsewhere the inner surface of the corolla bears no hairs or stipitate glands. The anthers are carried high enough in the corolla-tube to have their terminal appendage exserted from the corolla-mouth. From below the middle the anthers narrow towards an attenuate tip. The terminal 1.5 mm. of the anther, its appendage, consists of a sterile prolongation of the connective. This is narrowed to a slender point and is frequently curved to one side. It is the only part of the anther exserted from the corolla-tube. Although exserted, it does not become conspicuous, since it remains hidden behind the erect corolla-lobes which overtop it. The back of the anther has a broad, smooth, weakly convex connective which bears a very few stout closely appressed hairs. These hairs, unlike those on the anther in *Lasiarrhenum*, are few and inconspicuous and must be looked for under the microscope. At the base of the anther the thecae, though distinct for 0.6 mm. above the base, are not spreading but parallel. The lower end of each theca is acutish. Its tip never becomes appendaged or distinctly thickened as in *Onosma*. The style emerges from the fully developed corolla as its lobes unfold and soon bears its two stigmas 5–6 mm. beyond the tips of the erect corolla-lobes. Fruit of the plant is unknown. I am confident, however, that the nutlets will prove to be very similar to those of *Lasiarrhenum*.

4. **Lasiarrhenum** Johnston, Contr. Gray Herb. 70: 15 (1924). Type species *Onosma strigosum* HBK.

Plant perennial, prevailingly strigose, with spreading hairs only on the stem and veins of the leaf. Stems coarse, erect, several or more, simple or bearing ascending leafy floriferous branches above the middle. Leaves all cauline, numerous and usually crowded, elongate, triple-ribbed, narrowly lanceolate or the lower ones oblanceolate, those near the middle of the stem usually largest, those near the base of the stem small and even

imperfectly developed. Cymes scorpioid, always terminal, geminate on the main stem but usually single on the branches, in age straightening and elongating but remaining moderately crowded. Bracts numerous, linear to lanceolate, ascending, not very conspicuous even in fruiting inflorescences, scarcely if at all overtopping the adjacent fruiting calyx. Calyx 5-fid; lobes unequal with the abaxial one largest, acute, usually slightly more than half the length of the corolla, moderately accrescent in fruit; pedicel slender, straight, strictly ascending, half as long to as long as the calyx. Corolla white, regular, below the middle coarsely tubular and above the middle swelling to form a somewhat campanulate throat, the outer surface strigose; lobes erect, relatively small, more or less deltoid with the apex frequently rounded, as broad or broader than long, imbricate; throat on inner surface bearing scattered stipitate glands, frequently inconspicuously strigose along lines below the corolla-lobes, without faucal appendages; the annulus well developed, glabrous, a thick ridge or narrow collar, obscurely lobed. Filaments affixed at the base of the throat, nearly as long as the anther, thickish and somewhat fleshy, broad, dorsiventrally compressed, narrowly obovate to oblanceolate, usually bearing some stiped glands especially below the middle, but otherwise glabrous, below the attachment narrowly decurrent and forming thickened ridges on the walls of the corolla-tube. Anthers lanceolate, deeply included in the corolla-throat, attached distinctly below the middle, appendaged at the apex; terminal appendage evident, narrow, attenuate, compressed, base as broad as the connective of which it is an attenuate prolongation, with a length not exceeding and usually less than the maximum width of the dehiscent anther; base of anther lobed; thecae narrowing towards their apex, free for a short distance above the base, parallel or somewhat spreading at the lower end, the basal end usually acutish with a thickened tip; venter of anther glabrous, bearing the thecae closely juxtaposed, with the connective exposed only at the apex; dorsum of the anther with a broad connective, conspicuously hispid-villose both on the connective and on the back of the thecae, the hairs slender, white, loosely and antrorsely appressed. Pollen broadly but distinctly ovoid, 20–23 $\times$ 16–20 μ, broadest and bearing the pores about 8 μ above the broadly rounded base; lateral profile ovate, above the pores with the converging sides nearly straight and the apex abruptly rounded; polar profile circular; pores 7 or 8, usually obscure. Style emerging from the well-developed corolla-bud as the lobes unfold, shortly but distinctly surpassing the erect corolla-lobes; stigmas evidently two, diverging from the summit of the style. Nutlets smooth, white, lustrous, ovoid, narrowed at the base, all four frequently developing, divergent, on the venter bearing a low, rounded, weakly developed keel but no evidences of a ventral suture, dorsum convex; attachment scar basal, horizontal, nearly as broad as long. Gynobase broadly pyramidal, surmounted by the thickened persisting 4-angulate base of the style; attachment faces sloping, distinct, with thickened margins.

A very well marked genus with a single species, endemic to south central Mexico (Michoacan to Puebla and adjacent Jalisco to Oaxaca).

Lasiarrhenum strigosum (HBK.) Johnston, Contr. Gray Herb. **70**: 15 (1924).

Onosma strigosum HBK. Nov. Gen. et Sp. **3**: 93 (1818).
Onosmodium strigosum (HBK.) Don, Gen. Syst. **4**: 317 (1837).
Onosma trinervium Lehm. Asperif. **2**: 378 (1818) and Icones **1**: 11, t. 9 (1821).
Lithospermum longifolium Willd. in R. & S. Syst. **4**: 742 (1819).

Plant 5–10 dm. tall; stems abundantly short hispid with hairs 1–2 (–3) mm. long. Leaves at middle of stem 5–10 cm. long, 6–22 (usually 8–15) mm. broad, paler beneath, triple-ribbed, the strong midrib producing (about 10 mm. above its base) two evident strong, greatly prolonged assurgent veins, the veins nearly as strong as the midrib and extending almost to the leaf tip, evident on both sides of the leaf, hairs on the upper surface of the leaf provided with minute discoid bases but these seldom conspicuous. Corolla 15–23 mm. long, below the middle 3–4.5 mm. thick and subcylindric or slightly ampliate, at or slightly below the middle expanding into a campanulate throat 6–12 mm. broad at the top; corolla-lobes 3.5–5 mm. broad at the base, 2–3 mm. long. Filaments 3–5 mm. long, from the narrow attachment gradually expanding to become 1.3–1.5 mm. broad between the middle and the acute apex, arising 5–10 mm. above the corolla-base. Anthers 4–5.5 mm. long, 1–1.3 mm. broad below the middle, affixed 1.2–1.5 mm. above the base, reaching up to 1–3 (usually 2) mm. below the base of the corolla-sinus; terminal appendage 0.4–1 mm. long and 0.2–0.3 mm. wide at the base; base of anther held 1.5–3 mm. above the base of the filament; thecae free 0.5–1 mm. above the anther-base; dorsum of anther bearing hairs 0.6–1.3 mm. long, connective one third of the width of the anther. Style 16–23 mm. long, surpassing the corolla-lobes 1–5 mm. Nutlets ovoid, usually ca. 3 mm. long and 2.5 mm. thick, in transverse section with the ventral side broadly obtuse but elsewhere nearly circular in outline.

This monotype is particularly notable for its broad, fleshy, usually oblanceolate filaments and for its large lanceolate appendaged anthers which are coarsely and abundantly white-hairy on the back. In gross habit the plant is very suggestive of *Onosmodium*, a genus with which it was long confused. In floral structure, however, it is extremely different. The closest relations of *Lasiarrhenum* are with *Nomosa*. Details concerning this relationship are treated in the discussion of the latter genus.

The anthers of *Lasiarrhenum* have a somewhat less well developed terminal appendage than those of *Nomosa*, but otherwise are very similar as to form and size. Unlike the anthers of Nomosa, which bear only a few inconspicuous hairs on the connective, the whole of the dorsal surface of the anthers in *Lasiarrhenum* bears slender ascending white hairs in conspicuous abundance. The presence of hairs on the back of the anther is no common feature. Among American Lithospermeae they occur only in *Lasiarrhenum*, *Nomosa*, and one species of *Macromeria*, *M. viridiflora* DC.

The terminal appendage on the anther of *Lasiarrhenum* (and *Nomosa*) is very suggestive of that in *Onosma*, and because of this the possibility

has been recognized that our plant might have close affinity with that genus of the Old World. In structures other than the anthers, however, *Lasiarrhenum* and *Nomosa* have much more in common with *Onosmodium* and *Macromeria* The indications are that all these four genera are American derivatives of either *Lithospermum* or *Lithospermum*-like ancestors and so probably have no direct affinity with *Onosma*. The well-developed anther-appendages of *Lasiarrhenum* and *Nomosa* appear to be simply the extreme expression of the same tendency towards prolongation of the connective that is to be observed less well expressed in *Onosmodium* and *Macromeria*. In *Onosmodium* the connective is narrow, and the maximum prolongation of it, as in *O. unicum* Macbr. and *O. dodrantale* Johnston, is slender, weak, and at most 0.5 mm. long. The connective is also narrow in most species of *Macromeria*. In the one species of that genus, *M. viridiflora* DC., in which the connective approaches in width that of *Lasiarrhenum* and *Nomosa*, its prolongation is very short and stout. In *Macromeria* the thecae are equally broad from base to tip, and the anthers, accordingly, are more or less distinctly oblong in outline and have a broad summit. In *Onosmodium* the thecae are slightly narrowed above the middle and usually have an apiculate tip. The anther tends to have a lanceolate outline. In *Lasiarrhenum* and *Nomosa* the thecae are gradually narrowed to the apex. The anther as a whole is narrowed to the width of the broad connective at the level of the anther-tips, and the attenuate prolongation of the connective provides the pointed tip and thus completes the lanceolate outline of the whole anther.

5. Perittostema, gen. nov.

Herba parva perennis. Caules graciles erecti simplices strigosi foliosissimi. Folia gracilia lineari-subulata medio-costata sed enervata margine valde revoluta. Cymae scorpioideae solitariae glomeratae terminales. Bracteae lineares calyce breviores inconspicuae. Calyx 5-fidus; lobis ut videtur paullo inaequalibus cuneatis corolla plus quam duplo longioribus. Corolla lutea extus strigosa; tubo infra medium cylindraceo, supra medium in fauces subinflatos differentiato summum ad apicem (i.e., infra basim loborum corollae) paullo constricto; lobis tubi (faucibus inclusis) 5-plo brevioribus stricte adscendentibus paullo longioribus quam latis rotundis, in alabastro late imbricatis; faucibus quam parte inferiore cylindrico tubi subduplo crassioribus aequilongis, intus medium versus appendiculas invaginatas arcuatas glandulis stipitatis obsitas gerentibus; annulo vix elevato adpresse villuloso. Stamina in faucibus profunde inclusa. Filamenta basi faucium affixa, valde compressa, medio-costata, a basi angusta sursum valde gradatimque expansa, apicem versus latissima deinde abruptissime contracta, obovata vel deltoidea, subduplo longiora quam lata. Antherae oblongo-ellipticae filamento subduplo longiores paullo infra medium affixae apiculo attenuato recurvato terminatae basi bilobatae; thecis atro-marginatis quartem partem inferiorem distinctis et ibi sinu acuto separatis; connectivo late glabro laevi. Granulae pollinis ellipsoideae 24–25 $\times$ 20 μ, a latere visae ellipticae lateris angulatae, desuper visae circulares; poris

aequatorialibus 6–8 sed saepissime 7. Stylus gracilis lobos stricte adscendents corollae superans; stigmate terminali parvo obscure bilobo. Fructu ignoto. — Nomen derivatur a περιττος, insolitus, et στημα, stamen, quia filamenta formam anomalem habent.

Perittostema pinetorum (Johnston), comb. nov.

Lasiarrhenum pinetorum Johnston, Jour. Arnold Arb. **16:** 187 (1935).

Stems 10–15 cm. long, 2.5 mm. thick towards the base, internodes very short; leaves very numerous, 1–2 mm. broad above the base and very gradually narrowed towards the apex, linear-subulate, 10–30 mm. long, becoming gradually smaller upwards along the stem, bearing appressed stiff pallid hairs 0.3–0.5 mm. long, on lower surface all but the midrib hidden by the inrolling of the strongly revolute leaf-margins; cymes 3–7-flowered; calyx 4–4.5 mm. long, lobes ca. 0.7 mm. wide at the base, gradually narrowed; pedicel about 1 mm. long; corolla ca. 10 mm. long; tubular portion of corolla ca. 8 mm. long, below the middle cylindric and 2–2.5 mm. thick, above the middle expanding to form a swollen throat which becomes 3–4 mm. broad near its middle and then contracts to become 2–3 mm. thick at the summit; veins in the cylindric tube rather prominent; corolla-lobes ca. 2 mm. long and 1.8 mm. broad, rounded; faucal appendages arcuate, ca. 1 mm. broad, prominent, thickened and weakly invaginate, bearing some stipitate glands, included, borne 1.5 mm. below the constricted summit of the throat; anthers ca. 2 mm. long and 1 mm. broad, obtusish summit bearing a strongly compressed narrowly ligulate and strongly recurving terminal appendage which is 0.2 mm. long and nearly 0.1 mm. broad at the base; thecae free for 0.4–0.5 mm. above their base, in age somewhat spreading to form an open acute sinus at the base of the anther; base of anther held ca. 0.3 mm. above the base of the filament; apex of anther held 0.6–0.9 mm. below the summit of the corolla-throat, surpassing the faucal appendages 0.6–0.8 mm.; style 17–18 mm. long, surpassing the strict corolla-lobes ca. 2 mm.

A plant known only from the type collection now preserved in the herbarium at Paris. The specimen was collected by Ghiesbreght, no. 311, in September [? 1841] in temperate montane pine forests somewhere in Mexico. No geographical data were provided by the collector. Until the plant has been rediscovered, its home must remain subject to conjecture. I suspect that it is in the mountains of Oaxaca.

Although originally described as a species of *Lasiarrhenum*, the plant has no close relationship with that genus. Its closest affinities are with *Lithospermum*, and particularly with its Mexican species. It differs from the latter chiefly in its unusual filaments and in the form of the anther. From *Lasiarrhenum* it differs not only in habit and very narrow veinless leaves, but also in its rounded corolla-lobes, its faucal appendages, its ellipsoid pollen, and its glabrous anthers with dark-margined thecae and recurved terminal appendage.

Since the type collection is not a generous one and has only a relatively

few flowers, only two corollas have been available for dissection and close examination. Changes in the maturing corolla have not been studied, and the possibility that the corolla may be slightly zygomorphic has not been eliminated. The corolla-bud just before opening is ellipsoidal and at the base is prolonged downward into a short cylindric tube. At this early stage the swollen throat near its middle has a diameter about twice that at the summit of the throat (i.e., at the base of the broadly overlapping corolla-lobes), and more than twice that of the tube below the throat. The form of this corolla-bud is unusual in the Lithospermeae, indeed is approximated only in *Onosma* and *Maharanga*. The mature corollas retain their swollen throat, but this appears to be less constricted above the middle than previously. In the dissections available I find some indication that the mature corolla may possibly be somewhat prolonged on one side and may possibly have two of its lobes slightly larger than the other three. Inside the throat there are evident arcuate faucal appendages. These are formed partially by invagination and partly by thickening of tissue. They are dark in color and bear numerous but not crowded stipitate glands. It is to be noted that the appendages are borne not at the mouth of the corolla, at the summit of the throat, as in *Lithospermum*, but rather distinctly below the corolla-mouth, slightly above the middle of the throat, and hence are not exposed but are distinctly included in the throat.

The filaments of *Perittostema* are unique. They are firm in texture, dark in color, and very strongly dorsiventrally compressed. They gradually broaden upward from the narrow attachment and are broadest just below their truncate or broadly obtuse summit. In shape they are triangular or obovate-triangular. They measure usually about 1 mm. long and about 0.6 mm. broad across their summit. On the ventral side they have a small ridge down their middle. They are attached to the anthers by a small tip arising from the middle of their broad upper edge. These filaments of *Perittostema* are extremely different from those of *Lithospermum*, for in the latter genus the filaments are never laterally expanded and never other than linear, subulate, or unguiculate. The only member of the Lithospermeae with filaments even suggestive of those of *Perittostema* is the genus *Lasiarrhenum*. In the latter genus the filaments are compressed and are broadened upward, but are much larger and more elongate, being oblanceolate rather than triangular.

The anthers in *Perittostema* are relatively large for the size of the corolla and are accommodated within it largely because the throat is somewhat inflated. Although the anthers project above the level of the faucal appendages, their tips still fail to closely approach the mouth of the corolla. They are completely included. The open thecae have a dark-colored margin, an unusual feature which I have encountered among the Lithospermeae only in the genus *Halacsya*. For the lower quarter of their length the thecae are not joined together, and in age these tend to diverge, opening a deep acute sinus at the base of the anther. The broad summit of the anther is appendaged by a small but definite prolongation of the connective, which is unusual in being not straight but strongly recurved. In no

species of *Lithospermum* do the anthers evidently surpass the faucal appendages, nor do the anthers have a distinctly bilobed base. A few species of that genus have their anthers terminally appendaged, but when present the appendage is always straight and erect.

The pollen is ellipsoid, having the upper and lower half equal and the usually obscure pores, commonly seven in number, equally spaced about the equator. It is very similar to the pollen produced by species of *Lithospermum*, *Macromeria*, and *Psilolaemus*. That of *Lasiarrhenum* differs in its ovoid form.

The style is early elongate and before the corolla-bud opens is pressed upward and decurved against the still tightly imbricate corolla-lobes. It is promptly exserted and surpasses the corolla-lobes as soon as the latter unfold. In *Lithospermum* this behavior is duplicated in only a few species, all Mexican.

In addition to its floral structures *Perittostema* is also notable as a small plant with slender stems. Indeed, in these regards, among the Lithospermeae it is surpassed only by members of *Buglossoides* § *Rhytispermum*. Among American members of the tribe its slender stems and very slender leaves are approximated only by the Mexican *Lithospermum strictum*. The habit of *Macromeria*, *Onosmodium*, *Lasiarrhenum*, and most species of *Lithospermum* is very coarse and vigorous when compared with that of *Perittostema*. The leaves of our plant are extremely narrow and, *Lavendula*-like, have strongly revolute margins that roll back and cover all but the midrib on their lower surface.

6. **Psilolaemus, gen. nov.**

Planta perennis strigosa scabrella. Caules foliosi fruticulosi simplices vel laxe ramosi decumbentes vel adscendentes adpresse hispiduli e radice valida palari lignosa purpureo-tincta erumpentes. Folia omnino caulina sessilia firma valde costata enervata vel obscurissime paucissimeque nervata margine angusto-revoluta, facie superiore lucentia pilis rigidis brevibus saepe valde adpressis e discis pallidis erumpentibus instructa, facie inferiora breviter hispidula pilulis non rariter retrorsis donata, inferioribus oblanceolatis, superioribus lanceolatis. Cymae scorpioideae multiflorae solitariae caulibus ramisque foliatis terminatae maturitate rectae valde elongatae. Bracteae foliatae abundantes foliis supremis gradatim minores lanceolatae vel lanceolato-ovatae acutae pleraque calyce breviores. Calyx 5-fidus; lobis inaequalibus linearibus vel lanceolato-linearibus erectis, eo exteriore maximo. Corolla lutea ("armeniacea") tubulosa 3-plo longiore quam lata in parti tertiaria superiore gradatim ampliata alibi cylindracea, extus pilis minutis sparsis pleraque retrorsis donata, intus glaberrima nec appendiculis faucialis nec glandulis stipitatis praedita; lobis ovatis stricte adscendentibus supra basim latissimis quam longitudine corollae 6-plo brevioribus; sinibus limbi clausis basi nec incrassatis nec plicatis; faucibus angulatis lobis aequilongis, extus apice infra bases sinuum limbi gibbosis et infra bases gibbarum areolas depressas verticaliter elongatas apice maxime invaginatas gerentibus, inter areolas 5 depressas venis 3 prominulis

donatis; annulo obscuro glabro. Filamenta attenuata apicem versus faucium e plicis invaginatis faucium orientia supra medium exserta basi anguste breviterque decurrentia. Antherae oblongae 3–4-plo longiores quam latae utroque emarginatae nullo modo appendiculatae paulo infra medium affixae filamentis duplo longiores solum tertiam vel quartam partem inferiorem in faucibus inclusae, parte majore exsertae. Granulae pollinis ellipsoideae vel globoso-ellipsoideae 23–26 × 16–22μ, desuper visae circulares vel obscurissime polygonales, a latere visae ellipticae margine saepissime convexae poris obscurissime aequatorialibus (7 --) 8 donatae. Stylus gracilis evidenter exsertus, stigmatibus 2 distinctis terminalibus. Nuculae erectae parvae ellipsoideae albo-griseae laeves vel perinconspicue tuberculatae carinam ventralem versus utrinque profunde punctatae vel interrupte profundeque sulcatae, dorso convexae, ventre obtuse angulatae carinam latam vix prominentem proferentes, sutura obscura vel non rariter praesertim supra medium carinae inconspicue lineato-sulcata donatae. Gynobasis pyramidalis facies 4 planas adscendentes angulis prominentibus pyramidis separatas gerens basi incrasso styli terminata. — Nomen derivatur ab $\psi\iota\lambda o\varsigma$, calva, et $\lambda\alpha\iota\mu o\varsigma$, fauces, propterea quod fauces corollae glaberrimae et nec glandulis stipitatis nec appendiculis faucialis ornatae sunt.

Psilolaemus revolutus (Robins.) comb. nov.

Lithospermum revolutum Robins. Proc. Amer. Acad. **27:** 182 (1892).
Onosmodium revolutum (Robins.) Macbr. Contr. Gray Herb. **49:** 21 (1917).

Plant at first simple and erect but becoming branched and spreading in age; stems pale, 1–3 mm. thick, slightly fruticulose; leaves all cauline, with a strong conspicuous midrib which is sulcate above and prominent below; lower leaves largest, 3–7 cm. long, 6–15 mm. broad; cymes elongating, becoming 10–25 cm. long in age; calyx at anthesis 7–10 mm. long, weakly accrescent; pedicels ca. 1 mm. long at anthesis, becoming 2–4 mm. long in age; corolla 9–15 mm. long; tubular portion of corolla 7–12 mm. long, lower 9–10 mm. cylindric and 2–2.5 mm. thick, upper 2.5–3 mm. expanding to form a short throat 3–5 mm. thick at the summit; sinus between lobes closed above the base by the overlapping margins of adjoining corolla-lobes, neither thickened nor plicate at the base; corolla-throat outside with rather prominent veins and bearing five swellings and five depressions and hence somewhat angulate, bearing a small swelling directly below the base of each sinus of the corolla and bearing a small elongate depression (the complement of an inflexed plait inside the corolla) located directly under each swelling; stamens borne 0.4–0.5 mm. below the summit of the throat, arising from a small plait-like invagination of the corolla-wall; filaments 0.5–1.1 mm. long, exserted from the throat 0.1–0.5 mm.; anthers 1.4–2 mm. long, 0.4–0.6 mm. broad, oblong or slightly broader above the middle, emarginate at both ends, exserted from the throat 0.7–1.5 mm. but overtopped by the strictly ascending imbricate corolla-lobes and hence not conspicuous; style surpassing the corolla 1–2 mm., frequently emerging from corollas which have not yet attained maximum size; nutlets 2 mm. long and 1.5 mm. thick.

A plant known only from the gypseous saline marshes in southeastern San Luis Potosi, Mexico. As has been suggested by Macbride, Contr. Gray Herb. 49: 21 (1917), it shares characters with both *Lithospermum* and *Onosmodium*. Its closest relations, however, are with *Lithospermum*, with its Mexican species in particular.

Psilolaemus is distinguished from *Lithospermum* by the form of the corolla and the form and behavior of its stamens. The corolla-throat is angulate as in *Onosmodium* and as in that genus bears localized external swellings between the filament-attachments and the base of the corolla-sinus above. The stamens arise from small invaginations which are complementary to small elongate depressions on the outside of the corolla-throat directly below the subsinal swellings. In *Lithospermum* the corolla-throat bears invaginate appendages or stipitate glands or both, and the corolla-tube, sometimes hairy inside, always bears a basal annulus moderately to well developed. In *Psilolaemus* the annulus is very obscure and the inside of the corolla is completely glabrous and devoid not only of faucal appendages but also of all stipitate glands. The exserted style and the nearly erect corolla-lobes of the present genus are features duplicated in only a few of the many species of *Lithospermum*.

The plant has flowers resembling those of *Onosmodium* in being glabrous inside and devoid of stipitate glands and faucal appendages, as well as by having erect corolla-lobes, an exserted style, and an angulate throat with swellings below each corolla-sinus. It differs from *Onosmodium* in having elliptic pollen, oblong non-apiculate strongly exserted anthers, longer filaments, broadly and persistently imbricate ovate corolla-lobes, and closed corolla-sinus not thickened or plicate at the base. The leaves of *Onosmodium* are strongly veined. Those of *Psilolaemus*, as in most species of *Lithospermum*, are veinless or practically so. The style may be early exserted, but the flowers of *Psilolaemus* are not precociously sexual as in *Onosmodium*.

7. **Ancistrocarya** Maxim. Bull. Acad. St. Petersb. 17: 443 (1872) and Mel. Biol. 8: 543 (1872). Type species *A. japonica* Maxim.

Plant perennial, minutely strigose, stems fistulose, erect, simple. Leaves alternate, oblanceolate, evidently veined, all cauline; on lower half of stem small and imperfectly developed, deciduous at flowering time; on upper half of stem becoming very large and ample. Cymes scorpioid, 3–5, loosely disposed at the top of the stem, lowest one axillary, the others extra-axillary or terminal, simple, pedunculate, bracteate only towards the base, at maturity becoming stiff, straight elongate and loosely racemose. Calyx 5-parted, usually evidently pedicellate at least at maturity; lobes linear or sometimes oblanceolate, acute, erect, weakly costate, subequal or the abaxial one longest, about half as long as the corolla tube. Corolla lavender (becoming orange in drying), minutely strigose outside; tube subcylindric, length greater than the diameter of the limb, abruptly constricted at the base, upper portion not differentiated into a distinct throat, bearing no faucal appendages or glands, inside abundantly and antrorsely

villose-strigose above the middle; annulus represented by 10 tufts of hairs just above the base of the tube; lobes ascending, rounded, elongate, elliptic, imbricate in the bud; stamens included; filaments unguiculate, affixed at equal heights near the middle of the corolla tube, a third to a half the length of the anthers; anthers linear-oblong, affixed between the base and the middle, borne in the hairy upper middle third of the corolla tube, ends emarginate. Pollen small (20 × 12–13 μ long), elongate with rounded ends, constricted at the middle, encircled by a single row of 6 (– 8) inconspicuous pores about the broadest part of the broader lower half of the grain, polar profile circular or sometimes very obscurely polygonal. Style reaching up to the middle of the corolla-tube; stigmas 2, terminal, erect and ellipsoidal, juxtaposed and usually connate on the back below their middle. Ovary at anthesis 4-lobed, the lobes ellipsoidal. Nutlets smooth, lustrous, gray, elongate, obliquely lanceolate and conspicuously rostrate with the tip hamate, only one or two maturing, broadest just above the base and then very gradually attenuate into a very conspicuous slender laterally flattened strongly out-curving subulate beak with a hooked tip; venter of seminiferous lower half of nutlet distinctly convex, weakly or not at all keeled, lacking an evident suture; dorsum obtusish; attachment scar basal, large, slightly broader than long, flabelliform, bearing a conspicuous pit formed by the open funicular canal and (paralleling the dorsal edge) an arc of about 6 minor vascular strands. Seeds asymmetric, the lower end appearing obliquely truncate. Gynobase pyramidal when maturing more than a single nutlet, nearly as high as broad, with cartilaginous thickenings between the attachment faces and at the apex.

A very distinct monotypic genus of Japan especially notable for its very ample veined cauline leaves, its nearly bractless cymes, its corollas with the tube densely villous-strigose inside, and its elongate nutlets which are gradually attenuate into an elongate out-curved beak hooked at the apex. It appears to be most closely related to *Lithospermum*, which it resembles in pollen and in having broadly basifixed nutlets with a lustrous smooth pericarp.

Ancistrocarya japonica Maxim. Bull. Acad. St. Petersb. **17**: 444 (1872) and **20**: 471 (1875); Mel. Biol. **8**: 544 (1872).

Ancistrocarya japonica var. *albiflora* Honda, Bot. Mag. Tokyo **49**: 790 (1935).

Endemic to middle and southern Japan. The stems, branched only in the apical inflorescence, are 3–10 dm. tall. The underground parts are unusual and merit description from fresh material. They apparently consist of a congested sympodial rhizome that forms a crowded cluster of short, ascending, thickened, bulbose branches, each producing an aerial stem. No radical leaf-clusters are developed. The stems arise directly from the rhizome. The leaves are imperfectly developed at the base of the stem but rapidly increase in size as they are produced higher up along it and above the middle of the stem become unusually large and ample for an herbaceous borage, as much as 20 cm. long and 7 cm. broad. The

leaves of *Ancistrocarya* not only differ from other Lithospermeae in their large size but also in being conspicuously and loosely veined with the veins anastomosing.

Among the Lithospermeae the genus is also aberrant in its nearly bractless cymes. The lowermost flowers in the scorpioid cyme may be opposed by a small foliar bract 10–20 mm. long, and the second flower in the cyme may be subtended by a bract 1–3 mm. long, but the numerous later flowers are borne on a completely bractless rhachis. The cymes themselves have differing relations to stem-leaves. When more than two cymes are produced by the stem, the lowermost one is distinctly axillary and the others either distinctly supra-axillary or not at all intimately associated with a leaf. The two terminal cymes are usually about equal in development and may appear to be geminate. However, since no flower is borne in the fork at their base, they are simple cymes and not formed by the basal forking of a terminal cyme.

Superficially the corollas of *Ancistrocarya* much resemble those of the American species of *Lithospermum*, particularly so when seen in the herbarium. When dried they even assume an orange tonality similar to that presented by the orange or yellow corollas of the American plants in the same state. Unlike the American plants, however, *Ancistrocarya* has corollas that are lilac or bluish (or rarely white) when fresh. The radially symmetric corolla (11–14 mm. long in total length) has a well-developed tube 7–10 mm. long and 2.5–3.5 mm. thick, which is abruptly constricted to 1–2 mm. thick at the very base. At the summit it abruptly expands into the ascending corolla-limb. There are no markings nor constrictions of the tube to delimit the throat. The lower half of the tube is glabrous inside except for the ten tufts of hairs representing the undeveloped supra-basal annulus. The inner wall of the upper half of the corolla tube is clothed with abundant, antrorsely appressed, slender white hairs 0.5–1 mm. long. The filaments (0.8 mm. long), all equal and all affixed at the same altitude on the corolla, arise from amongst the hairs near the base of the villose-strigose upper portion of the corolla-tube. The anthers (1.5–2 mm. long) are accordingly mattressed dorsally by the dense indument on the corolla-walls; a condition paralleled among the Boraginoideae only in *Echiochilon*, *Sericostoma*, and one species of *Lithodora*. Another feature distinguishing the corolla from that of most species of *Lithospermum* is the complete absence of faucal appendages and stipitate glands.

In form, the nutlets of *Ancistrocarya* are unique, and furthermore the most bizarre in the family. They have a broad basal attachment and are broadest (ca. 2.5 mm.) about 1 mm. above their base. Above their broadest part they become gradually attenuate and prolonged into a strongly out-curving, laterally compressed subulate beak bearing a hook at the tip. Of their total length (7–9 mm.), only the lower half is seminiferous. Although the ovary is 4-lobed, only one or two of the lobes mature into nutlets, either a solitary abaxial one or an abaxial one and its adjacent axial companion. When two are developed they are somewhat divergent, for they are basifixed on adjacent faces of a pyramidal gynobase. The slender

hooked beak is strongly curved outward (away from the center of the flower), but the lower lanceolate seminiferous body of the nutlet is only very slightly so. The ventral side of the nutlet body is more rounded and swollen than the dorsal side. It develops no longitudinal ventral keel and furthermore bears no trace of a suture. The elongate, curved, subulate beak is a sterile apical prolongation of the pericarp, completely without parallel elsewhere in the Boraginaceae. Hooked at the tip it may function as an adaptation useful in animal dissemination.

8. **Buglossoides** Moench, Meth. 418 (1794). Type species *B. ramosissima* Moench. (= *Lithospermum tenuiflorum* L.)

Aegonychon S. F. Gray, Nat. Arrang. Brit. Pl. 2: 354 (1821). Based upon two species, *Lithospermum purpureo-caeruleum* L. and *L. arvense* L.

Rhytispermum Link, Handb. 1: 579 (1829). Based upon eight species, of which the first and third (*Lithospermum arvense* L. and *L. purpureo-caeruleum* L.) represent the present genus. The other six species mentioned belong to *Neatostema* (1 sp.), *Lithodora* (2 spp.), *Alkanna* (2 spp.), and *Rochelia* (1 sp.).

Margarospermum Opiz in Berchtold & Opiz, Oekon.-techn. Fl. Böhmens 2[2]: 73 (1839). Although Opiz cites *Lithospermum* § *Margarospermum* Reichenb. (1831) as a synonym, the description of his genus is based solely upon *Lithospermum purpureo-caeruleum* L.

Plant annual or perennial, herbaceous or fruticulose. Leaves veinless or nearly so. Cymes unilateral, simple or geminate or ternate, usually elongate, conspicuously bracted, usually racemose at maturity. Calyx 5-parted or 5-lobed, lobes narrow, at times united at the base to form a short cupulate tube, equal or unequal. Corolla blue, bluish, or white, funnelform or hypercrateromorph, outside usually bearing some appressed hairs, inside from the base of the corolla-lobes downward to between the tips of the anthers bearing five distinct longitudinal bands of hairs and/or glands or five hairy and/or glanduliferous inflexed plaits, below the insertion of the filaments naked or with five congregations of glands and sometimes with invaginate swellings, lobes spreading or ascending, imbricate; annulus near the base of the tube consisting of a narrow collar or ten scale-like lobes, frequently weakly developed and sometimes apparently absent; stamens borne at or below the middle of the corolla, included; filaments equal, affixed at equal heights on the corolla, shorter than the anther (usually about half as long); anthers lance-oblong or oblong, affixed at or slightly below the middle, base cordate, apex appendaged by a short prolongation of the connective; pollen small (15–25 μ long, 12–16 μ in diameter), cylindric or somewhat ovoid or rarely slightly elliptic, bearing the inconspicuous pores in a single row on or distinctly below the equator, in lateral profile with the sides usually straight or nearly so and either parallel or somewhat convergent towards the upper end; style not much if at all surpassing the anthers, usually much shorter than the calyx; stigmas two, rounded, borne laterally at the summit of the simple style or at the base on opposing sides of a short bilobed sterile apex of the style, usually evidently sub-

terminal; nutlets 1–4, erect to strongly divergent, smooth or rough, rounded or angulate, attachment basal or obliquely basal, ventral suture fused, obscure, sometimes prominent; gynobase flat or depressed pyramidal.

This genus is closely related to *Lithospermum* and is distinguished only by the structure of the corolla. In *Lithospermum* the corolla-throat may bear hairy and glanduliferous, invaginate, gibbose appendages or be variously glanduliferous or glabrous. The distinctive feature of the corolla of *Buglossoides* is the well-developed guides for insect visitors in the form of five distinct vertical bands of glands and stout hairs or five hairy and glanduliferous inflexed plaits. These guide-lines may be traced from the base of the corolla-lobes downward along a vein to between the anther tips or slightly above them. The gibbose invaginate faucal appendages present in many species of *Lithospermum* are also a feature of the flowers in many other genera of the Boraginaceae. The elongate inflexed plaits or the well-developed vertical bands of hairs and glands occur only in *Buglossoides*. Several other developments in the genus distinguish its species from most members of *Lithospermum*. These are the prevalence of blue as a corolla color, the apiculate anthers, the lobed sterile tip of the style, and the small size of the usually cylindric or ovoid-cylindric pollen grains. Singly, these latter features may occur here and there in species of *Lithospermum*, but never together nor in any species possibly a close relative of any species of *Buglossoides*. Floral dimorphy, in the form of heterostyly or cleistogamy, well developed in *Lithospermum*, does not occur in the present genus. Since the group gives every evidence of being a natural one, and since it can be readily distinguished from *Lithospermum* by well-marked, very unusual features of its corolla, it seems to merit generic recognition.

The stamens of *Buglossoides* are deeply included in the tubular portion of the corolla in all species except *B. purpureo-caeruleum*. In *Lithospermum*, stamens are borne at or below the middle of the tube only in species with a very abbreviated tube or in corollas of long-styled flowers of some heterostyled species.

The anthers are oblong or narrowly oblong and several times longer than broad and are borne on filaments half to a third of the anther length, in all species except *B. Gastoni*. In the latter the anthers are broadly oblong and only about twice as long as broad, and are borne on filaments nearly as long as the anther body. The largest anthers are those of *B. purpureo-caeruleum* and *B. Zollingeri*. These are 1–1.5 mm. long, twice the length of the anthers in other species. In all species the connective is prolonged to form a minute but definite tip on the anther. This tip may be subulate, cuneate, deltoid, or quadrate. It becomes as much as 0.2 mm. long in *B. purpureo-caeruleum*, but in other congeners it is usually only 0.1 mm. or less in length. It is least developed in *B. Gastoni*, in that species being stout, quadrate or deltoid, and scarcely projecting beyond the summits of the thecae. This tip on the anthers in species of *Buglossoides* is a character that separates the genus from practically all species of *Lithospermum*. The connective is prolonged apically in only a very few species

of *Lithospermum*, noticeably only in *L. tschimganicum* Fedtsch. of Central Asia and *L. papillosum* Thunb. and *L. cinereum* DC. of South Africa. Some of the Mexican species of *Lithospermum* have the anthers obscurely thickened at the apex but never to the degree found in *Buglossoides*. In most species of *Lithospermum* there is not even a vague suggestion of a terminal appendage.

The style is short. At anthesis it never reaches upward beyond the tips of the anthers. Rarely it may bear its stigmas between the anthers, but more commonly they are held below the level of the anther bases. In fruit the style is never more than half the length of the mature nutlets. In *Lithospermum* such short styles occur only in cleistogamic flowers or in the short-styled flowers of some heterostylic species.

The two stigmas are separated by the sterile tip of the style and are accordingly lateral and borne at or more commonly obviously below the style apex. The sterile tip of the style is commonly prolonged above the stigmas and is usually evidently bilobed. This condition is extremely well developed in *B. purpureo-caeruleum* and *B. Zollingeri*. In these two species the style tip projects beyond the stigma for a distance equal to or surpassing the diameter of the latter, and consists of two attenuate lobes. In *B. calabrum* and *B. Gastoni* the lobes of the style tip are shorter, stouter, and obtusish, but even so, they evidently project above the stigma. In the four species named, all members of the section *Margarospermum*, the stigmas are clearly subapical and well separated. Frequently the two stigmas are not equally well developed, and not uncommonly one may be borne slightly lower on the style than its companion.

Among the species of the section *Eubuglossoides* the style tips show greater variation. The two stigmas tend to be less sharply defined than in the section *Margarospermum*. In typical *B. arvense* the terminal lobes of the style may be cylindric or narrowly conic and always evidently surpass the stigmas. In *B. incrassatum* the lobes are evident, but usually less well developed than in *B. arvense* and its allied forms (e.g., *Lithospermum Sibthorpianum* Gris.) in the eastern Mediterranean area. In *B. tenuiflorum*, in most allies of *B. arvense* in northern Africa, as well as in plants referable to *L. minimum* Morris, the sterile tip of the style extends up between the stigmas but projects weakly if at all above them. The sterile tip of the style in these plants has either an unlobed truncate apex or an apex that is only obscurely lobed or merely notched.

The prolonged lobed sterile tip of the style in this genus needs investigation. Superficially the stigmas and the tip of the style, taken together, are very suggestive of the stigmatic head of the Heliotropioideae. It remains to be determined if the course of the vascularization is similar, cf. Hanf. Beiheft Bot. Centralbl. **54** [A]: 126 (1935). Among the Lithospermeae lobed style-tips are best developed in the present genus. In almost all species of *Lithospermum* the stigmas are terminal on the style, or if there is a prolongation of the style-tip between the stigmas it is only moderate and does not surpass the stigmas. Only in a few Mexican species (*L. Nelsoni*, *L. Berlandieri*, *L. mediale*, *L. oblongifolium*, *L. calci-*

cola, L. sordidum, and *L. distichum*) does the somewhat lobed style-tip ever project above the stigmas. However, in most of these species the style-tip is actually short and becomes prominent only because the oblong stigmas are widely spreading.

The pollen of *Buglossoides* is small and shows little variation in size from species to species. Though sometimes ellipsoidal or ovoid, its usual form is subcylindric or barrel-shaped, being circular in polar outline and commonly straight-sided or nearly so in lateral profile. Its pores, always in a single row, are extremely small and obscure, so much so that I have been unable to determine their number. In the section *Eubuglossoides* the pores are distributed around the grain exactly half-way between the poles, i.e., on the equator. The upper and lower halves of the grains are always similar in size and outline. In lateral profile the sides are usually straight and parallel and only occasionally somewhat convex. With proper lighting the grains may show a vague but definite narrow band about the equator. This equatorial band in which the pores are located has not been detected in any pollen of the other section of the genus. In the section *Margarospermum* the pores are borne perceptibly below the middle of the grain. The shorter lower portion of the grain (that below the line of pores) is usually perceptibly broader than the upper portion. In lateral outline the grains vary from oblong to more or less ovate, even within a single species. In profile they may have their straight sides practically parallel or very slightly convergent towards the upper end. Sometimes the sides are evidently convergent and the grain obviously somewhat ovoid. Frequently the grains show a very localized contraction just above the pores, with the result that they tend to develop short sloping shoulders which, though very much less well developed, are still recognizable as similar to the shoulders developed on the asymmetric pollen of *Lithospermum*, cf. Jour. Arnold Arb. **33**: 310 (1953). Such grains, narrowed very slightly in a zone above the pores (to form the shoulders), usually have their upper half with straight paralleling sides, but this portion is discernibly narrower than the shorter rounded basal portion. Accentuation of these tendencies would produce the strongly asymmetric grains of the footprint and hourglass type known in *Lithospermum*. In the genus *Buglossoides*, however, this tendency to develop shoulders on the grains is only very weakly expressed and frequently must be looked for before it is detected.

The distinctive corollas of *Buglossoides* have been illustrated and compared by Spengler, Oesterr. Bot. Zeitschr. **68**: 110 and 116, ff. 1, 2, 23–26 (1919). Synonymy for most of the species has been compiled by Stroh, Beih. Bot. Centralbl. **58** [B]: 203–4 and 206 (1938).

Section **Eubuglossoides.**

Lithospermum § *Rhytispermum* (Link) Reichenb. Fl. Germ. Excur. 336 (1831).

Plant annual or biennial, herbaceous; corolla small, 4–9 mm. long, white to blue, regular, inside bearing 5 vertical bands of glands or hairs but no

strongly inflexed plaits, lacking congregations of glands or invaginations directly below the stamen attachments; pollen symmetric, bearing the pores about the equator; style with or without a prolonged bilobed sterile tip; nutlets rough, usually all four developing, ventral keel prominent.

The corollas of species belonging to this section are more simply organized than those of the section *Margarospermum*. In the present section the walls of the corolla are only very slightly swollen beneath the five vertical bands of hairs and glands on its inner surface. Complementing these bands on the outside of the corolla are merely five shallow lineate grooves. Only an incipient tendency for invagination along the hairy vertical bands is accordingly present. In the section *Margarospermum* the invagination is very pronounced, and the hairs and glands clothe well-developed inflexed plaits that form the five intruding ridges on the inside of the corolla.

To be included in the section *Eubuglossoides* is *Lithospermum tenuiflorum* L., as well as *L. arvense* L. and the undetermined number of critical species all closely related to it.

Buglossoides tenuiflorum (L. f.) comb. nov.

Lithospermum tenuiflorum Linn. f. Suppl. 130 (1781).

A well-marked species which ranges from Greece east to Irak. The nutlets are distinctive. They have a very fragile pericarp. They are erect or slightly incurving and when *in situ* have their tips proximate and their ventral keels parallel. These nutlets are also smaller than those of *B. arvense* and its allies and are further differentiated by being distinctly constricted just above their smaller attachment surface. The cymes are short (even in maturity seldom more than 8 cm. long) and obviously geminate or ternate at the ends of the branches. The flowers (with a very small blue corolla) are always crowded and evidently biseriate on the cyme. The calyx does not develop a cupulate tube nor does it become enlarged abaxially as may be the case in *B. arvense* and its allies.

Buglossoides arvense (L.) comb. nov.

Lithospermum arvense L. Sp. Pl. 1: 132 (1753).

This species is either exceptionally variable or is a complex of minor species awaiting analysis by a monographer. The typical form is that with the largest flowers. Its white corollas are decidedly funnelform and evidently longer than the calyx. It is the form prevalent in middle and northern Europe and thence extends across Asia. In southern Europe and north Africa there are a number of distinguishable closely related plants, some of which are certainly geographically correlated and deserve specific recognition. Among these only *B. incrassatum* can be mentioned in the present paper. Others seem to merit recognition. Useful in distinguishing them from true *B. arvense* are differences not merely in habit but also in size, form, and color of corolla, size and form of the calyx lobes, degree of de-

velopment of the sterile style tip, and the presence or absence of a band of scattered short ascending hairs on the inner surface of the corolla just below the attachment of the stamens.

The fruit of *B. arvense* and its allies presents a number of very interesting features. The bony, hard, rough nutlets are straight and have a broad basal attachment which tends to become oblique. In the Boraginaceae nutlets with oblique attachments ordinarily have the attachment surface sloping upward towards the center of the flower and hence transgressing on the ventral side of the nutlet body. In *B. arvense* and its allies the reverse condition is true. If the nutlets are held in a vertical position, it is to be seen that the scar slopes upward, not towards the ventral but towards the dorsal side, and that as a consequence the nutlets are shorter on the dorsal side than on the ventral. Nutlets with an oblique attachment surface of this sort, when affixed to a low-pyramidal or nearly flat gynobase, are not erect with paralleling ventral keels, but are necessarily strongly divergent. This strong divergence of the nutlets of *B. arvense* and its allies is a development late in ontogeny. When they are young the nutlets are erect and parallel. They become noticeably divergent only as they approach full maturity.

Buglossoides incrassatum (Guss.) comb. nov.

Lithospermum incrassatum Guss. Ind. Sem. Hort. Boccad. 6 (1826); Fl. Siculae Prodr. 1: 217 (1827); Fl. Siculae Synop. 1: 217 (1842).

A close ally of *B. arvense* notable chiefly because of its remarkable calyx. After the fall of the corolla, the calyx, as it increases in size and the ensheathed nutlets mature, gradually becomes greatly modified in form as a result of excessive abaxial prolongation. At first the calyx is very similar to that of *B. arvense* at the same stage of development. It is affixed centrally on its symmetric base to the pedicel. At this early stage the central axis of the flower (or for all practical purposes, the style) points away from the leaf axil and is hence divergent from the stem. In later development, because of excessive growth on the abaxial side of the calyx-base, the axis of the flower is gradually shifted in an arc as great as 90° and finally points, not away from, but actually towards the adjacent stem. In other words the calyx is shifted from a central basal attachment to one that is distinctly lateral. The central line up the pedicel, if projected outward, no longer passes up the style but rather across the low gynobase, where it meets the style at an angle of as much as 90°. The mature nutlets are accordingly borne on a low gynobase which is now adaxial and which actually faces the adjacent stem. Because of the dislocation, the distorted calyx-base faces outward and so becomes the most conspicuous part of the fruiting calyx. The condition is unusual but not unique among the Boraginaceae. A very similar development is found in the genus *Pectocarya*, cf. Jour. Arnold Arb. 20: 400 (1939).

Various authors have dismissed the remarkable fruiting calyces of this species as teretological. With this I cannot agree. In *B. arvense* and other

near relatives of *B. incrassatum*, there is also a tendency for some enlargement of the fruiting calyx on the abaxial side and also a slight but definite tendency for the transverse axis of the gynobase to slope downwards towards the adjacent stem. In the present species these tendencies, merely incipient in its relatives, are developed excessively. The wide distribution of *B. incrassatum* about the Mediterranean area, where in many localities it appears to be the only representative of its group, is evidence that it is not a casual freak.

Section **Margarospermum** (Reichenb.) comb. nov.

Lithospermum § *Margarospermum* Reichenb. Fl. Germ. Excur. 337 (1831). Founded to include four species of which the first listed was *Lithospermum purpureo-caeruleum* L.; the other three are representatives of the genera *Lithodora* and *Moltkia*.

Plant perennial, herbaceous or fruticulose; corolla larger, 15–19 mm. long, blue or purple, the limb slightly oblique with the three abaxial lobes more spreading than the posterior two, inside bearing 5 vertical glanduliferous and/or hairy inflexed plaits and below each filament attachment bearing a congregation of glands and sometimes an invaginate swelling; pollen slightly asymmetric, the pores borne below the equator; style always with a bilobed sterile tip; nutlets smooth and lustrous or rugose, not strongly keeled, usually only one maturing.

This section includes only the four extremely well marked species enumerated below.

Buglossoides purpureo-caeruleum (L.) comb. nov.

Lithospermum purpureo-caeruleum L. Sp. Pl. **1:** 132 (1753).

Ranging from western Europe to Iran. Leaves usually broadest below the middle. Flowering stems clustered, arising from a densely branched rhizome, terminated by a pair of leafy racemose cymes. Corolla bearing faucal plaits 2–3 mm. long which originate 6–9 mm. above the base of the tube; also bearing distinct invaginate swellings 2 mm. long below each stamen; plaits glanduliferous but not hairy. Filaments attached 5–8 mm. above the base of the corolla; anthers ca. 1.5 mm. long, elongate, apiculate, twice as long as the filament. Style 8–9 mm. long, the sterile tips attenuate. Nutlets ellipsoidal, smooth, white, 3.5–4 mm. long, 3–3.5 mm. thick, back convex, venter obtuse.

The nutlets of this species are usually slightly larger but otherwise very similar to those of *B. Zollingeri* and *B. calabrum*. In being smooth, white, and porcelain-like, they much resemble the type of nutlet prevalent in *Lithospermum*. Unlike the nutlets of the other species of *Buglossoides* those of the present species have a relatively small basal attachment-surface which is located not at the center of the nutlet-base but rather on its ventral half. For notes on the habit of growth of this species see White, Jour. Bot. 22: 74–76 (1884).

Buglossoides Zollingeri (A. DC.) comb. nov.

Lithospermum Zollingeri A. DC. Prodr. **10:** 586 (1846).

A plant of Japan, China, and Korea. Leaves usually broadest above the middle. Flowering stems arising from procumbent stems persisting from the previous season, terminated by a simple unilateral cyme. Corolla on inner surface bearing glanduliferous, short-hairy inflexed plaits 4–5 mm. long which originate 5–6 mm. above the base of the tube, and also provided with short glanduliferous invaginate plaits below the attachment of each stamen. Filaments attached 3–4 mm. above the corolla base; anthers 1.5 mm. long, elongate, apiculate, several times as long as the filaments. Style 2–4 mm. long, the sterile tips attenuate. Nutlets ellipsoidal, 3–3.5 mm. long, smooth, white, back convex, venter obtuse or weakly keeled.

Collectors appear to have been aware of this plant only in its flowering state. Nearly a hundred collections of the species in American and European herbaria have been examined, but in this large suite only five collections show the plant in the fruiting state, and none of them bear nutlets that are completely mature.

Buglossoides calabrum (Tenori) comb. nov.

Lithospermum calabrum Tenori, Fl. Nap. **3:** 174 (1824–29).

Endemic in southern Italy. Leaves broadest at the middle. Flowering stems arising from slender procumbent stems persisting from the previous season, terminated by a simple racemose cyme. Corolla with a tube evidently much surpassing the calyx, inside bearing hairy, sparingly glanduliferous plaits 7–8 mm. long which arise 4–6 mm. above the base of the tube, below the filament attachments obscurely if at all invaginate. Filaments attached 2 mm. above the base of the tube; anthers almost 1.5 mm. long, elongate, apiculate, twice as long as the filaments. Style 1–2 mm. long, the sterile tips stout and obtuse. Nutlets ellipsoidal, smooth, white, 3.5 mm. long, 2.5 mm. thick, back convex, venter obtuse.

Buglossoides Gastoni (Benth.) comb. nov.

Lithospermum Gastoni Benth. ex DC. Prodr. **10:** 83 (1846); Bot. Mag. **47:** t. 5926 (1871).

Known only from the French slopes of the western Pyrenees. Leaves broadest below the middle, lanceolate. Flowering stems clustered, arising from a densely branched rhizome, terminated by a crowded densely flowered forked cyme. Corolla with hairy and glanduliferous inflexed plaits 3–4 mm. long which arise 2.5–3 mm. above the base of the tube, bearing no invaginations below the filament attachments. Filaments borne 1–1.5 mm. above the base of the corolla; anthers oblong, less than 1 mm. long, weakly apiculate, about as long as the filaments. Style 0.5–1 mm. long, the sterile tips stout. Nutlets yellowish, punctate and abundantly rugulose, very stout and plump, 4.5 mm. long and nearly as thick, keeled only about the sharp apex, attachment broad and basal.

A very distinct species differing from the other members of its section in having small anthers, very congested forked cymes, and very large, very plump, short-beaked, yellowish rugulose nutlets.

9. **Stenosolenium** Turcz. Bull. Soc. Nat. Moscou 13: 253 (1840); DC. Prodr. 10: 103 (1846). Type species *Anchusa saxatilis* Pallas.

Plant a hispid annual herb with one to many erect or decumbent stems. Leaves costate but veinless, lower oblanceolate, the upper ones becoming lanceolate. Inflorescence scorpioid, elongate, bracted throughout (lower bracts foliaceous), distinctly racemose in age. Calyx short-pedicellate, 5-fid, hispid; lobes slenderly lanceolate, attenuate, slightly unequal with the abaxial one usually the longest. Corolla violet or purple, salverform, outer surface with minute, short, usually spreading hairs, inner surface with a villulose annulus but otherwise glabrous, bearing no stipitate glands; limb spreading, breadth less than the length of the tube, rounded lobes slightly broader than long, imbricate in the bud; tube elongate, about twice as long as the calyx, subcylindric, upper third to half broadest and forming an ill-defined throat, above the base bearing a short thickish collar-like villulose annulus; throat unappendaged. Stamens borne at unequal heights in the throat, included, the uppermost one usually abaxial; filaments slender, a half to a third as long as the anther; anthers elongate, laterally compressed, affixed near the middle. Pollen elongate with rounded ends, symmetric, constricted at the middle, 38–41 × 22–25 μ (16–20 μ thick at the middle), bearing two rows of 8 or 9 inconspicuous pores one at each end of the grain, polar profile circular. Style shorter than the calyx, forked below the apex; stigmas two, distinct, compressed, obovate-spathulate. Gynobase flat or concave, with four triangular attachment faces, usually maturing four nutlets. Nutlets tuberculate, usually brownish, ascending, supported on a stout, laterally affixed inframedial vertical stipe; axial edge angulate, vertical, nearly straight, above the middle formed by the short ventral keel on the nutlet-body and below the middle by the ventral side of the stipe; seminiferous body of the nutlet ovoid, inclined at an angle of 40–45°, its pointed apex held above the nutlet-attachment and its rounded base abaxial to it; stipe stout, usually partially hollow, expanding abruptly at the base, sides minutely verrucose; funicular canal ascending vertically inside the stipe and entering the oblique nutlet-body near the middle of its ventral side; ventral keel short, supramedial, formed of a usually completely fused ventral suture. Seed straight, funicular attachment slightly above the middle.

A monotypic genus of eastern Asia. In most characters it shows close similarities with the Asiatic species of the genus *Arnebia* and is probably most closely related to them. Its fruit, however, is very different, not only from *Arnebia* but from all other members of the Lithospermeae.

Stenosolenium saxatile (Pallas) Turcz. Bull. Soc. Nat. Moscou 13: 253 (1840).

Anchusa saxatilis Pallas, Reise 2[3]: 718, t. "F", f. 1 (1773).

Onosma saxatile (Pallas) Lehm. Asperif. 2: 371 (1818).
Arnebia saxatilis (Pallas) B. & H. ex Forbes & Hemsl. Jour. Linn. Soc. 26: 155 (1890).

Ranging from the mountains near Pekin and northwestward across eastern Mongolia towards the Baical region.

The corolla is 12–19 mm. long in total length and has a spreading limb 7–10 mm. broad. The tube is 8–12 mm. long and its lower half or two thirds averages ca. 1 mm. thick. The upper half or third of the tube, however, is perceptibly thicker (ca. 1.5 mm.) and so forms an ill-defined cylindric throat. This elongate throat bears no hair nor glands on its inner surface and no appendages.

The stamens vary as to their distribution in the throat. In some plants they are affixed all at evidently different altitudes in the throat along most of its length, while in others they tend to be grouped below the middle of the throat, most of them with very slight differences in height of attachment and only one obviously higher than the others. When the stamens are loosely distributed, the uppermost stamen may be affixed 2–3 mm. above the lowermost one, but when crowded towards the base of the throat, the maximum difference in height of attachment may be reduced to 0.5–1 mm. The distribution of the stamens seems best described as spiral. Except that the uppermost one always appears to be on the abaxial side of the tube, the relative heights of the stamens seem to have no relation to any possible plane of symmetry in the corolla. The behavior of the androecium is suggestive of that in forms of *Arnebia decumbens*, cf. Jour. Arnold Arb. 33: 322 (1952). In that species the stamens may have a loose spiral arrangement in the corolla-throat or be grouped near the summit of the tube, sometimes with only one stamen attached obviously lower than the others. This grouping, when present, is at the top of the throat rather than at the bottom as in *Stenosolenium*, but the extreme range of variation in stamen attachment is otherwise very similar.

Although there are differences among plants as to the distribution of the stamens in the throat, the variation seems to be independent of any differences in style length. The forked style is always short, 3–5 mm. long, and reaches up into only the narrow lower half of the corolla-tube. The two compressed, somewhat spathulate stigmas are borne, accordingly, always well below the level of the lowest stamen. There is no evidence that either heterostyly or cleistogamy are ever present.

The pollen of *Stenosolenium* is elongate, constricted at the middle, with the upper and lower halves similar in size, form, and other details. At both ends, where broadest, it is encircled by a set of eight or nine equally spaced very conspicuous pores. These elongate, medially constricted, symmetric grains with biseriate pores closely resemble those of the species of *Arnebia*. Indeed, the only striking difference appears to be in the number of pores in each encircling row, eight or nine in *Stenosolenium* and four or five in *Arnebia*.

The nutlets of *Stenosolenium* are very distinctive. Viewed laterally, their seminiferous body (2 mm. long) is inclined about 45° and is supported

ventrally by a stout downwardly directed vertical stipe. This stipe is affixed obliquely below the middle of the sloping (ventral) under side of the nutlet-body and is short-columnar with the base ampliate and flaring. In lateral profile the nutlet has a vertical, nearly straight ventral edge (2 mm. high) which is formed above the middle by the short vertical ventral keel and below the middle by the ventral side of the stipe. Because of this the stipe appears to be a downward projection from the base of the short supramedial ventral keel. This keel, formed of a prominent fused ventral suture, ends abruptly. There is no suggestion of a downward prolongation onto the stipe below it. The stipe is minutely verrucose on all sides. Although distinct from the nutlet-body for most of its length, it remains close to the latter and its lower attachment end is in the same horizontal plane as the lower end of the body. Superficially, at first glance, the nutlet seems to have a strongly excentric but still basal attachment. A study of the course of the funicle, however, proves this is not the case. The funicle in its tubular canal is conducted upward from the gynobase inside the partially hollow stipe and then through the pericarp near the middle of the sloping ventral side of the nutlet-body. The important fact here is that the funicle enters the nutlet-body not at the base but below its middle on the side. In the strict morphological sense, the nutlets of *Stenosolenium* are laterally attached! Were the stipe on these nutlets suppressed and the attachment scar sessile, the latter would have a position almost half-way up on the venter of the nutlet. *Stenosolenium*, accordingly, has a character of the Eritrichieae.

The position of the attachment on the nutlet-body usually has phylogenetic significance and is the most important single character used in assigning genera to the tribes of the subfamily Boraginoideae. As an indicator of natural relationships it is prevailingly satisfactory, but as with all single characters, there can be expected to be instances in which its indications are not acceptable. Such seems to be the case as regards *Stenosolenium*. Only in the position of its nutlet attachment does that genus suggest the Eritrichieae. Other indicative structures all point to the Lithospermeae, and even more precisely to a close relationship with *Arnebia*. More significant than the nutlets in determining the affinities of *Stenosolenium* are its forked style with two stigmas, its unequally affixed stamens, its elongate corolla with well-developed basal nectary but unappendaged non-glanduliferous throat, and its elongate symmetric medially constricted pollen with two rows of pores. Only in *Stenosolenium* and *Arnebia* are these characters found associated. These and many other minor similarities seem to be unmistakable evidence of close affinity. *Stenosolenium* appears to be a member of the Lithospermeae, aberrant only in nutlet structure.

Among the Boraginaceae distinctly stipitate nutlets are developed in only a relatively few genera, in *Stenosolenium* and *Alkanna* of the Lithospermeae, in *Caryolopha* of the Anchuseae, and in *Plagiobothrys* § *Echidiocarya* of the Eritrichieae. Because it is partially hollow and has a dilated base, the stipe on the nutlets of *Stenosolenium* obviously differs in struc-

ture and appearance from those of the other genera mentioned. Surprisingly, the closest approximation is found in the obconic obliquely affixed attachment on the fossilized nutlets of the extinct *Prolithospermum Johnstonii* Elias, Special Paper Geol. Soc. Amer. **41**: 105, t. 15, f. 10 (1942) and Am. Midland Nat. **36**: 374–77, f. 3 (1946). These remarkably preserved nutlets, all that is known of the species, are found in middle Pliocene deposits of Kansas and Nebraska in middle United States. Thanks to Prof. Maxim K. Elias of the Nebraska Geological Survey, I have had a series of them for close study and comparison. They have a smooth, nearly erect, ovoid, slightly asymmetric body 2–2.5 mm. long, and on their convex side below the middle and above the rounded base bear a short, hollow, downward directed, basally expanding appendage with the attachment-surface on its horizontal base. This appendage is structurally similar to the stipe on the nutlets of *Stenosolenium*. Indeed, it differs only in originating less high on the side of the nutlet, in being shorter, and in being laterally adnate to the nutlet-body rather than free and slightly divergent from it. If the appendage on the nutlet of *Prolithospermum* were free rather than completely adnate laterally, it would be shorter, but would otherwise closely resemble the stipe in *Stenosolenium*. The homologies are so very clear that I am content to believe that the fossil plant belonged in a group ancestral to *Stenosolenium* and possibly even congeneric with it.

The nutlets of the extinct *Prolithospermum* give us an early stage in the evolution of the medio-lateral stiped attachment of the nutlets of *Stenosolenium*, and furthermore are suggestive of the manner by which it could have been originally evolved from a truly basal attachment on a *Lithospermum*-like nutlet. The attachment in our plants was probably evolved from a broad, horizontal, exactly basal attachment by shifting its center first to the ventral side of the nutlet-base and subsequently to a buttressed projection on the ventral side of the latter. As the attachment-surface, still large and still in relatively the same horizontal plane, became more and more to one side of the nutlet-base, the latter would cease to be truncate and would become more and more convex. The laterally dislocated attachment-surface could remain in the same relative plane only by buttressing its support higher on the ventral side of the nutlet-body. The combined results would place the attachment at the base of an obliquely affixed outgrowth to one side of the rounded base of the nutlet-body, precisely as is to be seen in the nutlets of *Prolithospermum*. A still further horizontal shift of the attachment would produce a still higher buttress on the nutlet venter and eventually even a "flying buttress" (i.e., the stipe) on the nutlets of *Stenosolenium*.

The peculiar feature of this support of the attachment in *Stenosolenium* and *Prolithospermum* is that it is more or less hollow. It is a tube-like or somewhat funnel-like organ which conducts the funicular canal from the flat gynobase upward to the point where it enters the nutlet-body. Accordingly it appears to be appendicular on the pericarp and not formed by constriction of the pericarp above the attachment or by localized gibbose prolongations of its walls, as in other stipitate nutlets. In various species

of *Lithospermum* and its relatives the attachment scar is surrounded by a projecting rim of pericarp. The nutlets of *Lithospermum incisum* provide one of the best examples of this. In that species the abscission is about the edge of the collar-like rim surrounding the centrally depressed scar. By modification of such a rim attachment the obliquely affixed suprabasal attachment support in *Prolithospermum* and the tubular support in *Stenosolenium* might have been evolved. If the ancestors of these two genera had such a rimmed attachment, the attachment, as it was shifted to a position off the nutlet base, could remain in the same horizontal plane by increasing the height of the rim, particularly so on the off side. Certainly the laterally adnate, more or less funnelform support of the attachment in *Prolithospermum* is very suggestive of some such origin. If such is the case, then the tubular support of the attachment in *Stenosolenium* is only a more advanced modification by which a rim about an attachment scar has become transformed into a hollow stipe.

The gynobase of *Stenosolenium* is flat and horizontal, or its four attachment pads slope slightly towards its center. On this gynobase a basifixed nutlet would be erect. A nutlet with a sessile lateral attachment would be oblique or horizontal. The peculiarities of the nutlets of *Stenosolenium* and *Prolithospermum* appear to be those modifications necessary if the large attachment on an originally basifixed *Lithospermum*-like nutlet was shifted from the base to a more and more lateral position while at the same time the body of the nutlets maintained an erect or nearly erect orientation and the flat gynobase continued unaltered. As the attachment shifted, the funicular canal within it would also be displaced and would enter the nutlet no longer at the base, but laterally. An increasing development of tubular stipe would be required for conducting the funicular canal upward from the flat gynobase, for the greater the horizontal shift of the actual attachment, the higher up on the venter of the nutlet body would become the point at which the funicular canal pierced the pericarp.

Change in position of attachment from basal to lateral, and even apical, is a progressive evolutionary trend responsible for much of the diversity of the fruit in the Boraginaceae. The various stages represent increasing degrees of specialization and in general are associated with the phylogeny of the groups in which they are illustrated. The tribe Eritrichieae has nutlets usually with lateral attachments. The fact that it has a higher evolutionary position than the Lithospermeae is suggested also by its more specialized corollas and other floral structures. In the Eritrichieae the development of lateral nutlet-attachment has been concomitant with the development of a pyramidal, spire-like or columnar gynobase. *Stenosolenium* and *Prolithospermum* have a funicle that enters the nutlet-body laterally, and hence, certainly in a morphological sense, have a lateral attachment. This character, however, appears to have had an origin independent of that in Eritrichieae, most likely as an aberrant development in the genus *Lithospermum*. It is an example of parallel evolution and not an indicator of relationships in the Eritrichieae. Unlike the condition in that tribe, the lateral attachment of *Stenosolenium* was developed un-

accompanied by compensating alterations of the gynobase, which has continued primitively flat as in *Lithospermum*.

10. **Arnebia** Forsk. Fl. Aegypt.-Arab. 62 (1775). Type species *A. tetrastigma* Forsk.

Dioclea Spreng. Syst. **1:** 502 and 556 (1825), not HBK. (1823). Type species *Arnebia hispidissima* (Lehm.) DC.

Strobila G. Don, Gen. Syst. **4:** 327 (1837). A renaming of *Dioclea* Spreng., not HBK.

Meneghinia Endl. Gen. 648 (1839). A renaming of *Dioclea* Spreng., not HBK.

Macrotomia DC. in Meisner, Gen. **1:** 281 and **2:** 190 (1840); DC. Prodr. **10:** 26 (1846). Type species *M. Benthami* (Wall.) DC.

Munbya Boiss. Diag. ser. 1, **11:** 114 (1849). Based on five species, the first two being forms of *Arnebia euchroma* (Royle) Johnston and the last three forms of *Arnebia densiflora* Ledeb.

Toxostigma A. Rich. Tent. Fl. Abyss. **2:** 86, t. 77 (1851). Based on *T. luteum* A. Rich. and *T. purpurascens* A. Rich., both forms of *Arnebia hispidissima* (Lehm.) DC.

Leptanthe Klotzsch, Ergebn. Reise Prinz Waldemar 95, t. 63 (1862). Type species *L. macrostachya* Klotz., a synonym of *Arnebia Benthami* (Wall.) Johnston.

Arnebiola Chiov. Fl. Somala 227, t. 24, f. 1 (1929). Type species *Arnebiola migiurtina* Chiov., a form of *Arnebia hispidissima* (Lehm.) DC.

Plants annual or perennial, herbaceous. Stems simple or loosely branched, arising from a taproot. Leaves all cauline or some in a basal cluster, numerous, veinless or in a few species with a few well-developed, greatly prolonged assurgent veins that parallel the midrib. Cymes scorpioid, simple or forked, terminal on the main stem and leafy branches and frequently also arising directly from the upper leaf-axils along the main stem, few to many, loosely to densely disposed, at times aggregated in dense corymbose or cylindric thyrsoid clusters terminating the main stems, in age remaining densely flowered or becoming loosely flowered. Bracts numerous, only rarely surpassing the adjacent calyx. Flowers heterostylic or monomorphic. Calyx lobed nearly to the base or 5-parted, weakly to strongly accrescent, in age sometimes developing a short swollen tube enclosing the ripening fruit, persistent or deciduous when the enclosed fruit is matured, usually shorter than the corolla-tube; calyx-lobes slender to coarse, linear, ligulate, subulate or lanceolate, in age sometimes prominently and coarsely veined and crested or papillate towards the base. Pedicels short, erect. Corolla regular or nearly so, yellow, cream, blue or purple, sometimes yellow with the limb conspicuously spotted with blue or black, salverform or rarely tubular, outer surface hairy or at least so on the outer surface of the limb; tube elongate, gradually ampliate or enlarging above the middle to form a cylindric throat; limb usually well developed, flat or broadly funnelform, narrow to broad; lobes strongly imbricate in the bud, usually rounded and about as broad as long, usually spreading or widely ascending, entire or sometimes with the margins

lacerate, erose or crisped; throat inside without hairs or faucal appendages and usually without any stipitate glands (stipitate glands when present very scattered and few, occurring about the mouth of the corolla, present only in some heterostylic species and usually only in the short-styled flowers); corolla-tube glabrous within or strigulose or villulose in two species only; annulus a papery collar, a thickened ring or completely absent, usually hairy. Filaments linear or unguiculate, usually very much shorter than the anther but in the short-styled flower of one heterostylic species nearly as long as the anther, affixed in the corolla-throat all at the same level or in one species at different levels. Anthers oblong to narrowly oblong, affixed at or slightly below the middle, in short-styled flowers and some monomorphic flowers borne high in the throat and frequently with their tips exserted, in long-styled flowers usually borne low in the throat and deeply included, apex emarginate or rounded or rarely acute, base rounded or rarely with the thecae somewhat pointed at the lower end, thecae usually joined down to the very base, connective narrow to relatively broad, not sulcate. Pollen elongate, 25–75 × 14–43 μ, in lateral outline oblong with rounded ends, the sides straight or more or less strongly incurving and the grains medially constricted, encircled by a row of pores at both the upper and the lower end of the grain, upper and lower half of the grain equal in size and configuration, polar outline circular, pores four or five in each row, obscure; in all heterostylic species the grains of long-styled flowers conspicuously smaller and more constricted medially than those of the short-styled flowers. Style slender, simple or simply forked or bis-bifid, included or shortly exserted; stigmas two or sometimes four, capitate, oblong or flabellate or rarely cylindric, simple or somewhat bilobed, juxtaposed and either strict or divergent at the apex of the simple style, or solitary and terminating the individual branches of the style. Nutlets one to four developing, erect, gray, brown, fulvous, greenish or rubiginous, never white nor porcelain-like, rough, never perfectly smooth, usually evidently tuberculate, verrucose, rugose or rugulose, surface usually dull, frequently minutely verruculose, papillate or muriculate; body of nutlet usually narrowing and more or less rostrate above the middle, sometimes conic-ovoid, conic-lanceolate or lance-ovoid and usually broadest below the middle and longer than broad, or sometimes more or less dorsiventrally compressed, much broadened below the middle and as broad or nearly as broad as long and ovate, triangular-ovate, or even cordate in dorsal outline; venter usually decidedly angulate, keel well developed or more or less obscure or well developed only above the middle of the nutlet; suture usually absent, when present usually obscure; dorsum frequently carinate above the middle, below the middle convex or medially depressed (in one species the dorsum plane or slightly concave and the venter convex); attachment basal, large, usually flabellate or ovate, rarely lobed, horizontal or somewhat oblique, occasionally prolonged upward for a short distance on the venter of the nutlet body, plane on the truncate base of the nutlet or sometimes margined by the downwardly prolonged pericarpial walls, rarely convex and protrudent

and visible even when the nutlet is viewed laterally. Gynobase flat or broadly pyramidal; attachment surfaces separated by lineate grooves, not margined by prominent cartilaginous tissue, plane or somewhat concave and sometimes very strongly upcurved ventrally to form a side of a frustum-like prominence at the center of the gynobase.

Arnebia as here defined includes the first fifteen species keyed and described in my recent study of *Lithospermum*, Jour. Arnold Arb. 33: 315–316 (1952), as well as four others discussed in a supplementary paper, op. cit. 34: 10–15 (1953). The well-known garden plant *Arnebia Echioides* (L.) DC. is excluded and assigned to the monotypic genus *Echioides*. As here accepted, therefore, the genus includes most of the species that have been traditionally assigned to *Arnebia* or its segregate *Macrotomia*. A few species of *Arnebia* extend into the drier portions of northern Africa, but most of the species in the genus are confined to Asia.

Over a year ago *Arnebia* was considered only in relation to *Lithospermum*, and after an evalution of its characters it was merged with that genus. Returning to *Arnebia* and *Lithospermum* after having critically examined all the other genera of the Lithospermeae, I find myself judging the two genera not merely by the number and decisiveness of characters useful in distinguishing them, but also according to the degree of phyletic divergence they represent as compared with that given generic recognition elsewhere in the Lithospermeae. It is now apparent that the amplified *Lithospermum* includes greater morphological extremes and is accordingly a relatively more comprehensive unit than other genera recognized within the tribe. Since I believe that genera within a natural circle of relationship should be roughly equivalent in value, it now seems best to abandon my broad concept of *Lithospermum* and reclassify its species under three smaller, more homogeneous genera (*Lithospermum*, s. str., *Arnebia*, and *Echioides*) that represent units of evolutionary divergence comparable with those given generic recognition elsewhere within the tribe.

Arnebia and *Lithospermum* are very closely related but evidently represent diverging phyletic lines. The characters they share are more numerous than their differences. The intimacy of their relationship is evidenced by unusual morphological features present in precisely the same form in both genera. Especially notable is the heterostyly in many of their species. This heterostyly, occurring in diverse species-groups in both genera, is of the most advanced sort, involving not merely dimorphy in corolla-form, stamen-attachment, anther-size, style-length, and pollen-size, but also pollen-form. The latter feature is unknown in other heterostylic plants and may be unique. This unusual development as an indicator of affinity becomes especially significant when it is recalled that heterostyly is uncommon in the Boraginoideae and that elsewhere in the Lithospermeae it is developed in only one other genus, in a very simple form in *Lithodora*. A minor feature, also rare in this family and among the Lithospermeae, developed only in *Arnebia* and *Lithospermum*, is the lobulate, lacerate, or strongly crisped margins of the corolla-lobes. A few very dissimilar species in both genera share this character.

The difficulties in separating *Arnebia* from *Lithospermum* have been discussed at length, Jour. Arnold Arb. 33: 310–315 (1952). As has been noted, the only decisive character useful in distinguishing them involves pollen morphology. Other possible differences have occasional exceptions or are difficult to express. The fruit has evolved differently in the two genera, but the differences cannot be concisely stated. The corolla-throat in *Arnebia* is never decorated with faucal appendages as is frequently the case in *Lithospermum*, and seldom, and then only very sparingly, does it bear stipitate glands comparable to those always present, usually in abundance, on the corolla-throat of *Lithospermum*. Some developments present in only some species of a genus are also indicative. The annulus inside the corolla, extremely well developed in some species of *Arnebia*, is completely lacking in others. In *Lithospermum* the annulus, weak to moderately well developed, is always present. The forked style, frequently present in *Arnebia*, is unrepresented in *Lithospermum*. The subterminal stigmas, frequent in *Lithospermum*, do not occur in *Arnebia*. The evanescent dark-colored spot on the corolla limb, developed by various yellow-flowered species of *Arnebia*, occurs also in *Echioides* but not in *Lithospermum*. With only one exception, all species of *Lithospermum* have corollas that are yellow, orange, or white. In *Arnebia* the corolla has a greater range of colors, including not only yellow and orange, but also blue, pink, and brown. Seven of the eighteen species of *Arnebia* are very definitely herbaceous annuals. Of the forty-four species of *Lithospermum* only two are plants of short duration, and these may be biennials or very short-lived perennials.

Since I discovered that *Arnebia* has very different pollen from that of *Lithospermum*, cf. Jour. Arnold Arb. 33: 308–311, f. 1–32 (1952), I have examined the pollen in all the other genera of the Lithospermeae. I am now of the opinion that the differences in pollen are much more important than previously realized. Pollen of a type similar to that of *Arnebia* has been encountered only in *Stenosolenium*. It differs from that in all other genera of the Lithospermeae in bearing two rows of pores, one at each end of the grain. The grains are always elongate and are symmetrical with the upper and lower half similar in size and configuration. In all other genera of the tribe, including *Lithospermum*, the pores are in a single row and the grains vary from symmetrical to very asymmetrical. The lower half of the grain is frequently much larger and more rounded than the upper half and hence different in configuration. No evidences of transition between the two types have been detected. The pollen in *Arnebia* (and *Stenosolenium*) has unusual and distinctive features and is the most extreme type in the Lithospermeae.

During my study of the Lithospermeae I have become increasingly impressed by the prevailing constancy as to type that is exhibited by the pollen within the various genera of the tribe. Within a given genus pollen may be very uniform in all species or it may present a limited number of variations which are all modifications of a single basic type. Closely related genera usually show close similarities in pollen. Other than in the

amplified *Lithospermum* (including *Arnebia*), now abandoned, I found a single type of pollen or modifications of a single type in all genera except *Moltkia*. In that genus § *Echianthus* has globose-ellipsoidal grains with six to eight equatorial pores. In § *Eumoltkia*, however, the globose grains appear to have about twenty pores, these not lined up about the equator but arranged, rather, in a strongly undulate line that crosses the equator diagonally at four places. The precise description of the pollen of § *Eumoltkia* is impossible with my technique, but in any case I am sure that the pollen in this section differs more from that in § *Echianthus* than is customary within the genera of the Lithospermeae. Even so, the differences are less fundamental than those between the pollen of *Arnebia* and that of *Lithospermum*. It is therefore not inconsistent to emphasize the pollen differences separating *Arnebia* and *Lithospermum* and to use them in bolstering the less decisive macroscopic differences in justifying my present recognition of both these genera.

The eighteen species of Arnebia have been described and discussed, their synonymy listed, and keys provided for their identification, in two previous papers of this series, Jour. Arnold Arb. 33: 315–334 (1952) and 34: 7–16 (1953). In the reports mentioned the species were treated as members of the genus *Lithospermum*. Their correct names as members of *Arnebia* are given below.

Section **Euarnebia.**

Corolla subtubular; lobes erect, triangular, acute, longer than broad. Stigmas four, elongate, cylindrical. Nutlets plano-convex with a cordate base, dorsum plane or very slightly concave, venter broadly convex, lacking a ventral keel; attachment surface three-lobed, the scar of the dorsal vascular traces located in the sinus of the cordate nutlet-base much more conspicuous than that of the funicular canal. Plants annual. Corolla without annulus.

1. **Arnebia tetrastigma** Forsk. Fl. Aegypt.-Arab. 63 (1775); Johnston op. cit. 321 (1952).

Section **Strobilia** (G. Don), comb. nov.

Corolla with a well-developed spreading limb, lobes rounded, spreading, about as long as broad. Stigmas usually two, capitate or oblong or flabellate. Nutlets with a rounded back, an angulate keeled venter, and a broad base, attachment surface not lobed, the scar of the dorsal vascular traces less conspicuous than that of the funicular canal.

** PLANTS ANNUAL; COROLLA WITH ANNULUS.*

2. **Arnebia decumbens** (Vent.) Coss. & Kralik, Bull. Soc. Bot. France 4: 402 (1857); Johnston, op. cit. 322 (1952).

3. **Arnebia hispidissima** (Lehm.) DC. Prodr. 10: 94 (1846); Johnston, op. cit. 325 (1952).

4. **Arnebia Griffithii** Boiss. Diag. ser. 2, 3: 135 (1856); Johnston, op. cit. 326 (1952).

5. **Arnebia fimbriopetala** Stocks in Hook. Jour. Bot. & Kew Miscl. 3: 180, t. 6 (1851); Johnston, op. cit. 7 (1953).

6. **Arnebia minima** Wettst. in Stapf, Denkschr. Acad. Wiss. Wien **50**: 30 (1885); Johnston, op. cit. 327 (1952).

7. **Arnebia linearifolia** DC. Prodr. **10**: 95 (1846); Johnston, op. cit. 328 (1952).

*** PLANTS PERENNIAL.*

× COROLLA WITH ANNULUS.

8. **Arnebia fimbriata** Maxim. Bull. Acad. St. Petersb. ser. 3, **27**: 507 (1881); Johnston, op. cit. 328 (1952).

9. **Arnebia obovata** Bunge, Mem. savants étrang. St. Petersb. 7: 407 (1851); Johnston, op. cit. 329 (1952).

10. **Arnebia Szechenyi** Kanitz, Pl. Exped. Szecheny 42, t. 5 (1891); Johnston, op. cit. 329 (1952) and 8 (1953).

11. **Arnebia guttata** Bunge, Ind. Sem. Hort. Dorpat. p. vii (1840); Johnston, op. cit. 330 (1952).

12. **Arnebia Lindbergiana** (Rech. f.), comb. nov.

Macrotomia Lindbergiana Rech. f. Ann. Naturhist. Mus. Wien **58**: 58 (1951); Johnston, op. cit. 10 (1953).

×× COROLLA WITHOUT ANNULUS.

13. **Arnebia densiflora** Ledeb. ex Nordmann, Bull. Acad. St. Petersb. 2: 312 (1837); Johnston, op. cit. 331 (1952).

14. **Arnebia inconspicua** Hemsl. & Lace, Jour. Linn. Soc. **28**: 326 (1891); Johnston, op. cit. 12 (1953).

15. **Arnebia euchroma** (Royle) Johnston, Contr. Gray Herb. **73**: 49 (1924); Johnston, op. cit. 333 (1952).

16. **Arnebia Benthami** (Well. ex G. Don), comb. nov.

Eichium Benthami Wall. Numerical List no. 931 (1829), nomen; G. Don, Gen. Syst. **4**: 333 (1838); Johnston, op. cit. 333 (1952).

17. **Arnebia speciosa** Aitch. & Hemsl. Proc. Linn. Soc. **18**: 81 (1880); Johnston, op. cit. 13 (1953).

18. **Arnebia nobilis** Rech. f., Ann. Naturhist. Mus. Wien **58**: 58 (1951); Johnston, op. cit. 14 (1953).

11. **Echioides** Ortega, Tabulae Botanicae 7 (1773); Johnston, Jour. Arnold Arb. **33**: 314 (1952). Type species, *Arnebia Echioides* (L.) DC.

Aipyanthus Stevens, Bull. Soc. Nat. Moscou **24**: 599 (1851). Type species *Arnebia Echioides* (L.) DC.

Plant perennial. Stems several, erect, simple below the inflorescence. Leaves borne along the stem and in basal clusters, uppermost ones with rounded or subcordate sessile bases, basal ones oblanceolate; midrib prominent but veins usually evident only on the basal leaves. Cymes scorpioid, simple or forked, terminal on the stems, in age elongating, becoming straight and racemose. Bracts numerous and conspicuous, foliaceous, usually evidently surpassing the adjacent calyx, lanceolate, asymmetric with the base rounded or subcordate. Calyx lobed almost to the base; lobes moderately unequal, cuneate-linear to narrowly lanceolate, shorter than the corolla-tube, accrescent; pedicels short, stout, erect. Flowers strongly heterostylic. Corolla yellow, villulose outside, with an elongate cylindric or weakly ampliate tube which towards its summit abruptly expands into the short open throat and the spreading limb; limb with a diameter about equaling the length of the tube, bearing five evanescent brown or blackish spots, one at the base of each sinus; lobes widely spreading, rounded, about as broad as long; throat open, shallow, glabrous, without stipitate glands or faucal appendages; tube villulose inside, without glands; annulus absent. Stamens borne in the tube at several superimposed levels, in the long-styled flowers within a zone below the middle of the tube and in short-styled flowers in a zone just below the summit of the tube; filaments linear, very short, one fourth to one fifth the length of the anther; anther narrowly oblong, affixed at or just below the middle, emarginate at base and apex, dorsum with a relatively broad connective that is sulcate above the middle; thecae separate for a short distance above their bases but remaining parallel and juxtaposed. Pollen spherical or very slightly longer than broad, bearing nine obscure pores about the equator, 30–35 μ in diameter in short-styled flowers and 40–50 μ in long-styled flowers. Style slender, half as long or as long as the corolla-tube, somewhat thickened directly below the terminal stigma; stigma deeply bilobed, the lobes joined at the base and becoming divergent. Nutlets large, very plump, ovoid or elliptic-ovoid, prominently and narrowly keeled on the venter but elsewhere convex, tawny and finely mottled with purple, opaque, smooth or sparsely and broadly low-tuberculate, ventral suture absent; attachment scar basal, large, plane, usually margined by the weakly protrudent pericarpial walls. Gynobase broadly pyramidal, the attachment faces flabellate, plane, sloping, margins not upturned nor thickened, adjacent faces separated by a groove.

A monotypic genus native to Armenia, the Caucasus, and adjoining northern Iran.

Echioides longiflorum (C. Koch), comb. nov.

Arnebia longiflora C. Koch, Linnaea 20: 640 (1849).
Lycopsis Echioides L. Sp. Pl. ed. 2, 199 (1762).
Arnebia Echioides (L.) DC. Prodr. **10**: 96 (1846).
Aipyanthus Echioides (L.) Stevens, Bull. Soc. Nat. Moscou **24**: 600 (1851).
Arnebia cyrousiana Parsa, Kew Bull. 1948: 211 (1948) and Fl. l'Iran **4**[1]: 221 (1952).
Lithospermum cyrousianum (Parsa) Johnston, Jour. Arnold Arb. **34**: 7 (1953).
Lithospermum Tournefortii Johnston, Jour. Arnold Arb. **34**: 7 (1953).

The present plant has been traditionally classified as an *Arnebia*, this with considerable justification, for indeed it does have many similarities with that genus. Its pollen, however, differs extremely from that of *Arnebia*, being very similar in type to that characteristic of *Lithospermum*. In this regard the plant destroys the universality of the one set of characters that might be used in separating *Arnebia* and *Lithospermum* in a decisive manner. Because decisive characters could not be found, I recently merged *Arnebia* and *Lithospermum*, Jour. Arnold Arb. 33: 311–315 (1952). The amplified *Lithospermum* produced I now recognize is more heterogeneous than other genera of the Lithospermeae. In order to reestablish *Arnebia* and have it separated from *Lithospermum* by at least one crucial character, and at the same time have both genera homogeneous, it has been necessary to exclude the present plant from both of the genera mentioned.

Although *Echioides* shares many characters with *Arnebia* and *Lithospermum* it differs from both in the attachment of the stamens in its strongly heterostylic flowers. The stamens within a flower are borne at several different altitudes above the corolla-base, being irregularly distributed within a broad zone inside the corolla-tube. This staminiferous zone is located below the middle of the corolla-tube in long-styled flowers and just below its summit in the short-styled ones. In *Arnebia* the stamens may be borne at unequal distances above the corolla-base in *A. decumbens*, but that is not a heterostylic species. In both *Arnebia* and *Lithospermum* the stamens in all heterostylic species are always whorled. In having the irregularly distributed stamens confined to a zone on the corolla that varies in position according to whether the individual is long- or short-styled, the present plant differs from all other members of the Boraginaceae and may even be unique among all heterostylic plants.

The corolla of *Echioides* as to general form is more suggestive of species of *Lithospermum* than of those of *Arnebia*. The corolla-tube, in having hairy inner surfaces, finds its closest parallel among American species of *Lithospermum*. In having a naked throat the corolla agrees with that of *Arnebia* and is very different from that of *Lithospermum*, for in the latter genus the throat is always decorated with faucal appendages or stipitate glands. The complete absence of the annulus is also suggestive of *Arnebia*. The annulus is suppressed in some species of *Arnebia* but is always present in some form in all species of *Lithospermum*. Most suggestive of *Arnebia*, however, are the five transitory dark spots decorating the yellow corolla-

limb, a very attractive feature usually present, which *Echioides* shares with only four or five species of *Arnebia*.

The large plump nutlets suggest those of *Lithospermum* in form but differ from that genus in their tawny mottled opaque surface. Their surface features are more like those of nutlets in Arnebia. The pericarp is not dotted with pits, nor does it bear a row of pits and slots paralleling each side of the ventral keel. These are features regularly present on the nutlets of many species of *Lithospermum* but never developed in *Arnebia*. The attachment faces on the gynobase are flat and separated by a groove. They do not have thickened margins, nor are they separated by prominent cartilaginous ridges. The gynobase, accordingly, is of a type universal in *Arnebia* but relatively uncommon in *Lithospermum*. The pollen grains of *Echioides* are spheric and have nine pores arranged about the equator. They are, hence, extremely different both as to form and type from the elongate grains with biseriate pores which are universal in *Arnebia*. Although much larger than those of any species of *Lithospermum*, the grains of *Echioides* are the same as to type. In form and general organization they are duplicated by several species of *Lithospermum*.

12. **Lithospermum** L. Sp. Pl. 132 (1753) and Gen. Pl. 64 (1754). Type species *L. officinale* L.

Batschia Gmel. Syst. **2:** 315 (1791); Rehder, Kew Bull. **1935:** 396 (1935). Based on *Anonymos caroliniensis* Walter, Fl. Carol. 91 (1788), which represents *Lithospermum caroliniense* (Walt.) MacMill.

Cyphorima Raf. Am. Monthly Magazine **4:** 191 and 357 (Jan. and March, 1819) and Jour. de Phys. Chem. Hist. Nat. **89:** 98 (Aug. 1918); Merrill, Ind. Raf. 202 (1949). ". . . le type du genre est le *Lithospermum latifolium* de Linné [*L. latifolium* Michx.!]. Les *Batschia longiflora* et *decumbens* (Nuttall) doivent peut-être s'y rapporter?"

Pentalophus A. DC. Prodr. **10:** 86 (1846). Based on *L. longiflorum* Spreng. and *L. mandanense* Spreng., both forms of *L. incisum* Lehm.

Plants distinctly perennial and arising from a strong, frequently dye-stained taproot or rarely short-lived and springing from a slender biennial or perhaps even annual root. Stems herbaceous or rarely somewhat fruticulose, simple or more or less branched, hispid, villose or strigose, erect or spreading, short to elongate. Leaves usually numerous, sometimes pinnately veined but more commonly veinless, occasionally in a sterile basal cluster but usually all cauline. Cymes scorpioid, simple or geminate, few- to many-flowered, borne terminal on the stems and branches or sometimes also in the uppermost leaf-axils and becoming aggregated into a cylindrical thyrse, usually elongating, straightening and becoming racemose in fruit. Bracts usually numerous and surpassing the adjacent calyx, foliaceous. Calyx 5-fid, the lobes linear-cuneate or lanceolate, short to elongate, usually evidently shorter than the corolla-tube, the abaxial one usually appreciably the largest; pedicels very short to elongate, strict or ascending and rarely decurved. Flowers monomorphic or strongly heterostylic, rarely cleistogamic. Corolla regular, yellow, orange, or white (or pinkish or bluish

to purple-red in one Chinese species), hairy on the outer surface, salverform, funnelform, or cylindric; tube straight, usually elongate, subcylindric or gradually ampliate or more commonly enlarging at or above the middle to form a differentiated throat; limb usually spreading or broadly ascending, small to large, its diameter less than, equal to, or surpassing the length of the corolla-tube; corolla-lobes equal, strongly imbricate in the bud, usually orbicular to ovate but sometimes semicircular or obovate, spreading or loosely ascending or rarely strictly ascending and nearly erect, margins entire or rarely lacerate, crisped or erose; corolla-throat frequently bearing small invaginate pubescent or glanduliferous appendages and always bearing some stipitate glands either generally distributed or localized in a band or in congregations; faucal appendages when present weak to well defined, trapeziform, lunate, gibbose, or merely convex; corolla-tube glabrous inside or sometimes distinctly hairy; annulus usually evident and usually hairy, a tumid band, a narrow ring, or represented by ten quadrate or gibbose lobes or rarely reduced to 5 to 10 tufts of hairs. Stamens arising at or usually well above the middle of the corolla-tube, borne below the middle of the tube only in long-styled flowers of some heterostylic species. Filaments unguiculate or linear, usually half the length of the anther or less, longer than the anther in one species only, all affixed at the same height above the corolla base, usually hidden behind the anther, never exserted, glabrous and glandless or sometimes bearing a few glands on the decurrent base. Anthers small, oblong to narrowly oblong, usually compressed laterally, included or rarely with the tips exposed in the corolla mouth, rounded at both ends or with the tip obscurely apiculate, affixed at or near the middle; connective on dorsum usually narrow; thecae united to the base or free for only a very short distance above the base, parallel and closely juxtaposed throughout. Pollen isodiametric or more commonly longer than broad, 13–42 μ long and 8–42 μ broad, spheric or barrel-shaped or ellipsoid with the upper and lower halves of the grain equal in size and configuration, or ovoid or medially constricted with the upper and lower halves very dissimilar in size and configuration, in heterostylic species grains of long- and short-styled flowers differing in size and frequently also in form; pores 6 to 9 but most commonly 8, borne in a single row about the equator or about the lower half of the grain where it is broadest. Nutlets erect, usually ovoid or ellipsoid and plump, broadest at or below the middle, gradually narrowed to the base or sometimes suprabasally constricted to form a stout neck just above the broad flaring base or sometimes with a thickish collar about the base; apex usually obtusish, dorsum convex (flattened below the middle in one species); venter convex or somewhat obtuse, its medial keel rarely sharp, usually low and rounded and sometimes obscure, the ventral suture lineate or obscure; surface of nutlet usually polished and porcelain-like, white or somewhat stained with brown, rarely verrucose or rugose or tumulose, usually completely smooth or smooth with few to numerous punctate depressions, the depressions sometimes shallow but usually deep and pit-like and frequently on the venter of the nutlet elongating to become slot-like, a well-defined row of

slots or pits or both frequently present on both sides of the ventral keel and parallel to it; attachment of nutlet large, basal, plane, convex or in one species excavated, horizontal or somewhat oblique, the end of the broken funicular canal usually evident near the ventral angle, near the middle of the dorsal half of the attachment the ends of the dorsal vascular supply marked by a dot, a swelling, or by an erect or ascending subulate or peg-like process. Style slender, simple, included in the corolla-tube or sometimes exserted; stigmas 2, usually distinct, globose, hemispheric or ellipsoid, usually small, terminal and juxtaposed on the tip of the style or subterminal and separated by the short, somewhat bilobed sterile tip of the style. Gynobase flat to broadly pyramidal, sometimes surmounted by a thickened angulate persisting base of the style; attachment faces flat or slightly concave (or saucer-shaped or cupulate in one species), horizontal or ascending, plane or the margins somewhat thickened and prominent, separated by a groove or by the thickened protrudent angles of the gynobasic pyramid.

In the past the genus *Lithospermum* has been very broadly defined. As one of the relatively few original Linnean genera of the family it early became a catch-all for a great variety of plants subsequently recognized as generically separable. During the past century its history has been one of shrinking limits. As here defined the genus is further shrunk and I believe at last reduced to homogeneity. Various diverse elements still included in the genus by recent classifiers I have excluded and treated under such genera as *Buglossoides*, *Lithodora*, *Psilolaemus*, *Moltkia*, *Moltkiopsis*, *Mairetis*, and *Neatostema*. Also excluded are *Echioides* and *Arnebia*, recently included in the genus in my "Survey of the Genus Lithospermum," Jour. Arnold Arb. 33: 299–363 (1952). My reasons for now excluding these two latter will be found discussed under *Arnebia*.

Lithospermum, as here accepted, includes forty-three of the fifty-nine species treated in my recent paper on the genus. The first fifteen species in the "Survey" are now referred to *Arnebia*, and species no. 17 (*L. Tournefortii*) to *Echioides*. To be added to the forty-three species keyed and described in the "Survey" is one other species that was improperly excluded. This is *L. cinerascens* of Peru and Ecuador, which will be discussed presently. The genus *Lithospermum* as now defined contains, accordingly, a total of forty-four species.

The genus is especially notable for its floral dimorphism and its diversity of pollen forms. For a discussion of these and various other details the reader is referred to the above-mentioned "Survey."

Lithospermum, among all the genera of the Lithospermeae, is the only one with representatives on all continents. Of the forty-four species, four (*L. officinale*, *L. erythrorhizon*, *L. tschimganicum*, and *L. Hancockianum*) are native to Eurasia, one is confined to the highlands of tropical Africa (*L. afromontanum*), four occur in South Africa (*L. papillosum*, *L. diversifolium*, *L. cinereum*, and *L. scabrum*), and five are indigenous to the highlands of northwestern South America (*L. cinerascens*, *L. Macbridei*, *L. mediale*, *L. peruvianum*, and *L. Gayanum*). The remaining thirty

species occur in the United States and Mexico, with the greatest concentration in the latter country. Among the species in the Old World the most distinct is *L. Hancockianum* of southwestern China. The other species of the Old World have not only the technical characters, but the facies of the species in America, and were they natives of the New World would be accepted in *Lithospermum* without question. The interrelation of the species of Europe, Africa, and America is very clear and strong, and the genus, despite its wide distribution, is a very satisfactory and natural assemblage

The genus is not only notable for its wide distribution and particularly for its occurrence in both Old World and New but also for the number of other genera with which it seems to be closely related. It is the only genus in the Lithospermeae which has close generic affinities in both America and the Old World. The genus has affinity with all the genera of the tribe native in America and is very closely related with *Macromeria*, *Perittostema*, and *Psilolaemus*. In the Old World its closest affinities are with *Arnebia*, *Echioides*, and *Buglossoides*, and perhaps also *Lithodora*. Its affinities with other Old World genera are only very generalized, certainly not immediate.

The wide distribution of the genus and the number and distribution of genera closely related to it suggests that perhaps *Lithospermum* may be a relatively generalized conservative old stock from which many of the modern Lithospermeae may have been differentiated. Such a conclusion, however, is difficult to reconcile with the fact that *Lithospermum* in many features shows specializations not to be expected in a primitive group. The modification of the corolla-throat is noteworthy in this regard. In other tribes of the Boraginoideae, all without doubt containing more highly evolved plants than the Lithospermeae, faucal appendages, usually invaginate and frequently very elaborate, are features of the corolla in practically all genera. It is interesting to note, therefore, that among the twenty-three genera of the Lithospermeae, well-developed faucal appendages are developed only in *Perittostema* and in various species of *Lithospermum*. Elongate plaits in the throat, possibly homologous with the faucal appendages of other genera, occur only in *Buglossoides* and *Macromeria*, both closely related to *Lithospermum*. Stipitate glands in the corolla-throat, localized and usually abundant, which appear to have some relation with the development of faucal appendages in the Lithospermeae, occur only in *Lithospermum* and its close relatives (*Macromeria*, *Lasiarrhenum*, *Perittostema*, *Arnebia*, and *Lithodora*). The corollas of most genera of the tribe have no faucal appendages and bear no stipitate glands in the throat. Among genera evidently related to *Lithospermum* this is also the case in many or all the species of *Macromeria*, *Onosmodium*, *Psilolaemus*, *Nomosa*, *Lithodora*, *Arnebia*, and *Echioides*. Modifications of the corolla-throat are features developed only in *Lithospermum* or to some degree only in genera evidently related to it. As a complex elaboration of the corolla, it seems to indicate that the genus is a highly specialized member of the Lithospermeae and not a generalized conservative one.

A high position in the evolution of the Lithospermeae is also indicated for *Lithospermum* by the elaborate development of heterostyly among various groups of its species. Heterostyly of a precisely similar sort is also present among certain groups of species in *Arnebia* and in a slightly more complicated state in *Echioides*. Elsewhere in the tribe it is developed only in *Lithodora*, and there in only a very simple form. The condition, accordingly, occurs in the Lithospermeae only in *Lithospermum* and in genera evidently related to it. Heterostyly, like the elaborations of the corolla, gives reason for believing that *Lithospermum* is an advanced member of its tribe.

The nutlets of *Lithospermum* are prevailingly plump, ovoid or ellipsoid, and usually obtusely pointed, and have a convex dorsum and a venter that is merely obtusely angled or obtusely angled with a low rounded medial keel. Nutlets with a narrow sharp ventral keel occur only in a few species, e.g., *L. strictum* and *L. Hancockianum*. Only in *L. strictum* is the dorsum of the nutlet distinctly flattened. The surface of the nutlet is prevailingly lustrous and porcelain-like, white or somewhat stained with brown. It is completely smooth or smooth with scattered pits usually most abundant on the ventral surface. Tumulose, rugose, or verrucose nutlets occur only in *L. papillosum* and *L. cinereum* of South Africa and in *L. Parksii* and *L. mirabile* of Texas and adjacent Mexico. The only species with smooth nutlets that are not lustrous is *L. indecorum*.

A distinctive minor feature of the nutlets of *Lithospermum*, evident to some degree in most species of the genus, is the two vertical lines of deep pits or deep slots in the pericarp which parallel the ventral keel. One of these lines of depressions is usually present along each side of the keel, close to its lateral base or only a short distance removed. Outside of *Lithospermum* the lines of pits or slots associated with the ventral keel have been observed only in *Psilolaemus* and in one species of *Onosmodium*, *O. virginianum*. Possibly they may also occur on the nutlets of *Nomosa* or *Perittostema*, but at present the fruit of these genera is unknown. In any case they do not occur in *Arnebia*, *Echioides*, *Macromeria*, and *Lasiarrhenum*. In *Buglossoides* they are not developed in § *Margarospermum*, though possibly comparable developments may be present in § *Eubuglossoides*. Interestingly, they are present in *L. Hancockianum*, that very distinct species of unusual habit native to eastern China, which, of all species of *Lithospermum*, is most suggestive of *Arnebia*.

The nutlets usually narrow gradually towards the broad base or towards a constriction just above the base. In some species the suprabasal constriction forms a stout neck just above the flaring base of the nutlet. In others the suprabasal constriction is weak, but below it the nutlet is modified and has a more or less collar-like base. The scar is usually broad, distinctly basal, and horizontal or somewhat oblique. Towards the ventral edge of the scar the broken end of the funicular canal is usually evident either as a pit or as a short section of protruding tube. The lower end of the vascular supply to the dorsum of the nutlet may be undifferentiated or be marked by a small convexity near the middle of the dorsal half of

the scar. Commonly, however, the tissue about the ends of the dorsal traces protrudes to form a small process on the scar. It is usually ascending and subulate in form but sometimes is peg-like and erect. Although in various genera related to *Lithospermum* there is frequently a modest elevation of tissue about the dorsal traces, when present it is usually less extreme than that to be encountered on the base of the nutlets in many species of *Lithospermum*. Indeed, outside of *Lithospermum* well-developed processes were noted only on the nutlets of *Macromeria viridiflora*. The most extreme elevation of tissue about the dorsal traces occurs on the nutlet base of *L. incisum*. In that species the process is relatively coarse, peg-like, and vertical, and because the surface of the scar collapses it gains in apparent height and becomes conspicuous in the excavated lower end of the nutlet. A similar, less extreme development of the peg-like process also occurs on the nutlet of the related species *L. Parksii*. The feature is probably a compensatory development associated with the elaboration of the broad collar-like base distinctive of the nutlet in these species, although strangely in *L. mirabile*, the other close relative of *L. incisum*, the nutlet base is flat and the process is very weak and short. The well-developed peg on the nutlet attachment of *L. incisum* is associated with another unusual feature of that species. When the nutlet detaches, the withdrawal of its peg leaves a central depression on the attachment face of the gynobase. After the fall of the nutlet the attachment face shrinks and assumes a cupulate form that is unique in this genus. Although the peg on the nutlets of *L. Parksii* is almost as prominent as that in *L. incisum*, its fall leaves no central depression on the attachment faces of the gynobase. In *L. Parksii* the faces remain permanently plane and are similar to those of other species in the genus.

A species deserving of special comment is *Lithospermum cinerascens* (DC.) Johnston, Contr. Gray Herb. **75**: 40 (1925), originally described as *Macromeria cinerascens* DC. Prodr. **10**: 69 (1846). This plant, a native of the mountains of Ecuador and northern Peru, was excluded from *Lithospermum* in my recent study of that genus. I have subsequently had all the representation of the species preserved at Kew and the British Museum (collections of Mathews, Jameson, and Lobb) available for close study and comparison, and am now of the opinion that the species is closely related to *L. guatemalense* of northern Guatemala and adjacent Mexico, and congeneric with it. The South American plant is distinguishable from *L. guatemalense* and all other members of its genus by its elongate filaments, these being once and a half to twice as long as the anthers. The corolla appears to be rather variable as to size and form. It is 3–4.5 cm. long. The elongate tube is gradually expanded for most of its length or it swells and becomes somewhat cylindric above the middle. Just below its summit the tube abruptly expands and is there somewhat funnelform. From its edges arise the short (3.5–5 mm.) ovate or ovate-triangular corolla-lobes. The lobes are usually ascending, but in one collection of Lobb there is indication that they may sometimes be reflexed. The anthers are borne in the open funnelform mouth of the tube, their tips barely if at all pro-

truded from it. The slender filaments, 3–5 mm. long, arise 4–6 mm. below the tube summit. The medio-affixed anthers, 2–3 mm. long, are oblong and bear a pair of minute tips on their rounded summits. The thecae are joined to the very base. The corolla-tube bears scattered stipitate glands in a band 2–4 mm. broad just below the tube summit. There are no faucal appendages. The annulus consists of ten quadrate glabrous lobes. The lustrous white nutlets are sparsely punctate and bear pits and slots in a line on both sides of the ventral keel. The stigmas are subterminal and are separated by the very short and stout bilobed sterile apex of the style. The pollen is broadly ellipsoid, 25–28 × 22–24 μ, and has eight obscure pores on the equator. In large-flowered plants the trumpet-shaped corolla of the species is suggestive in size and form of that of the genus *Macromeria*. Though the filaments are more elongate than in all other species of *Lithospermum*, they are definitely included within the corolla-throat, as is characteristic in that genus. They are not exserted from the corolla-throat, as are the filaments in all species of *Macromeria*. The anthers are also included, or at most have only their tips exserted. The well-developed annulus in the corolla is that of *Lithospermum* and not *Macromeria*. The nutlets also have features of *Lithospermum*. They are punctate and bear pits and slots in a row on either side of the ventral keel, which is never the case in *Macromeria* but is frequent in *Lithospermum*. The plant gives no evidence of being closely related with any particular species of *Macromeria*. It does, however, have an evident ally in *Lithospermum* in *L. guatemalense*. Between *Macromeria* and *Lithospermum*, the plant clearly belongs in the latter genus.

13. **Cerinthe** [Tournef.] L. Sp. Pl. 136 (1753) and Gen. Pl. 66 (1754). Type species *C. major* L.

Annual, biennial, or perennial herbs, glabrous or nearly so, sometimes glaucescent. Stems leafy, one to numerous, simple or branched, usually erect. Leaves all cauline or some in basal clusters, glabrous or at most with very scattered appressed hairs or a ciliolate margin, with inconspicuous pinnate veins, upper surface usually dotted with pallid groups of mineralized cells; lower cauline leaves more or less oblanceolate but usually broadened at the very base and usually with a somewhat amplexicaul attachment; middle cauline leaves oblong or ovate, sessile, with a broad cordate-auriculate amplexicaul base, apex usually obtuse or rounded. Inflorescence loosely scorpioid, elongating and unilaterally racemose in age; cymes single or geminate at the ends of the stems and branches; bracts very well developed, foliaceous, very conspicuous, sometimes purpurescent, usually hiding the calyx, base cordate-auriculate and amplexicaul. Calyx 5-fid; lobes very unequal, strongly imbricate, foliaceous or somewhat membranous, glabrous or with margin ciliolate, usually accrescent in age, outermost sepal broadest and usually somewhat cordate at base; pedicel slender, glabrous or short hispidulous, in age elongate, ascending or decurved. Corolla yellow or partially purple or violet, completely glabrous, coarsely tubular, several times longer than broad, broadest

at or above the middle, straight and regular or most prolonged on the two-lobed adaxial side with the tube ventricose and the limb more or less distinctly oblique; throat without appendages, hairs or stipitate glands; annulus evident, a narrow thickish glabrous ring or collar; lobes broadly to narrowly triangular, very short or as much as two thirds the length of the tube, more or less recurved or sometimes erect or even connivent, acute or the tip somewhat rounded. Filaments affixed above the middle of the corolla-tube, glabrous, usually thickish and narrowed from a broad base, equal or within the corolla differing slightly in shape (odd medial stamen adaxial), less than a quarter the length of the anther to nearly as long. Anther elongate, affixed above the base, included in the throat or more than half exserted from it, free or joined only by entangling of the tails on the thecae, terminated by an evident gradually narrowed sterile appendage; terminal appendage usually with a narrow tip, frequently with a denticulate margin; thecae with minutely papillate-ciliolate edges, near the base remaining separate and tending to spread and thus form the more or less sagittate base of the anther; basal end of theca sometimes with only a short stout thickened tip but more commonly with the tip prolonged into a slender flexuous barbellate tail; back of anther pale or frequently black, more or less coarsely muricate or muricate-papillate, connective usually smooth and only moderately prominent. Pollen barrel-shaped or ellipsoid to nearly spheric, 18–37 × 15–33 μ, polar profile circular or somewhat polygonal; pores eight, borne in a well-developed equatorial groove, rarely prominent; colpi eight, fusiform or linear. Ovary four-lobed, four-ovulate. Nutlets one or two, each two-celled (one-celled or one-ovulate only by abortion), smooth, rarely lustrous, usually mottled with brown or purple, erect or weakly incurved, more or less broadly ovoid, back convex, apex notched and bicuspid, venter flattened and not keeled; suture linear-sulcate, evident on the venter of the nutlet and frequently also down the dorsum and rarely even across the attachment scar; attachment broad, basal, plane. Gynobase strongly depressed, when fully developed bearing two semicircular to near circular attachment faces which are horizontal or are slightly inclined away from the base of the style. Style slender, eventually exserted from the corolla, dorsiventrally compressed at the base; stigmas two, small, terminal, juxtaposed, distinct or more or less united.

A very distinct and readily recognizable genus with representatives occurring from middle Europe and northwest Africa east to the Caucasus and northern Iran. No detailed comprehensive treatment of its species has been published. The genus contains at least three or four major species and also a goodly number of well-marked geographic varieties that are accepted as species by many authors. *Cerinthe* has its greatest concentration of forms in the western and northern portions of the Mediterranean area.

Among the Boraginoideae *Cerinthe* is notable for its practically glabrous herbage, its usually broad leaves and bracts that are cordate-amplexicaul at the base, its very strongly unequal broadly imbricate calyx-lobes, and

especially its bilocular two-seeded nutlets. The plant is obviously a member of the Lithospermeae, and though very highly specialized and distinct, probably has its closest affinities with *Onosma* and related genera.

In general structure and appearance the corolla and androecium are very similar to those of *Onosma* and *Podonosma*. The corolla-lobes may be short and recurving as prevalent in *Onosma* or elongate and erect as in *Podonosma*. Although the corolla is completely glabrous and thus different from many of the species in *Onosma*, corollas that are glabrous or very scantily pubescent are found in *Podonosma* and in some species of *Onosma*. The stamens of *Cerinthe* show a prevailing basic similarity with those of *Onosma* and its relatives. The elongate anthers are terminated by a similar terminal appendage. They are also roughened on the back, and their thecae are also free and more or less spreading at the base. The lower end of each theca may have a thickened point as in *Onosma* or, unlike in that genus or in any of its allies, may be prolonged into a slender flexuous barbellate tail. Unlike in the genera mentioned, the anthers are joined neither by coherence at the base of the thecae nor by coherence along the margin of the thecae. The anthers of *Cerinthe*, though regularly free in some species and varieties (as in *Onosma*), in most species are held together at the base — not by growing together, but only by the entangling of the flexuous tails on the thecae. The synandrium produced, though not achieved by adnation, functions exactly like that in those species of *Onosma* which have only the basal tips of their thecae coherent.

The corolla of *Cerinthe* may be perfectly regular or have a more or less clear bilateral symmetry. In *C. retorta* Sibth. & Sm., and to a less extent in some of the forms of *C. major* L. and its allies, the corolla may be more or less distinctly ventricose, not only above the base on the abaxial side, but also above the middle of the adaxial side. When this is relatively well developed, as in *C. retorta* and *C. gymnandra* var. *macrosiphonia* Murb., the unilateral swellings can so modify the form of the corolla that it becomes weakly curved in a sigmoid manner. In the two plants mentioned, the corolla is slightly prolonged on its two-lobed adaxial side, and the upper portion of the tube is somewhat outcurved and the limb is oblique. Associated with this zygomorphy of the corolla is also some differentiation among the filaments inside. In *C. gymnandra* var. *macrosiphonia*, furthermore, the exserted cone of connivent anthers is not central and vertical in the mouth of the corolla, but rather, emerging from the abaxial side of the mouth, is directed obliquely upward, with the tip over the opposite side of the corolla-limb. The flowers of *C. retorta* and *C. gymnandra* var. *macrosiphonia* have an evident bilateral symmetry that has involved not only the corolla but also the androecium. Among the many species of *Onosma* the only parallel to the conditions described in these species of *Cerinthe* is that in *O. multiramosum* H.-M. of China. In that species the matured corollas in the bud and the exserted synandrium in the open flowers are prolonged on the adaxial side and are strongly out-curved, i.e., bent away from the cyne axis in a manner suggestive of the subapical out-curving of the corolla observable in *Cerinthe*.

The fruit of *Cerinthe* differs from that of all other Boraginoideae in having bilocular two-seeded nutlets and these never more than two in number. The two carpels of the fruit, which in other Boraginoideae are each divided to form a pair of distinct one-celled one-seeded nutlets, are unlobed in *Cerinthe*. The nutlets are superficially similar to the two-seeded nutlets produced by some species of *Heliotropium* and are comparable also to the two-seeded pyrenes of the drupaceous fruits of some Ehretioideae. For the proper interpretation of the fruit of *Cerinthe* the evolutionary steps in the development of fruit within the Boraginaceae should be recalled. The fruit in this family has been elaborated from a two-carpellate, two-celled ovary bearing four ovules which become four-celled by the development of a partition within each carpel, and then, subsequently, become two-lobed and then four-lobed, and finally in the Boraginoideae become four-parted, with each lobe (the nutlet) unilocular and one-seeded and affixed independently about the base of the style. Since the two-seeded nutlet of *Cerinthe* represents a whole carpel, and the one-seeded nutlets of all other members of the Boraginoideae only half of a carpel, it is perhaps not surprising that the fruit of *Cerinthe* has been interpreted by some authors as being not only the most simply but also the most primitively organized within the subfamily, and even as more or less transitional to the less highly evolved fruits in the Heliotropioideae and Ehretioideae. With such a conclusion, however, I cannot agree. Along with most authors, I am of the opinion that the two-seeded nutlets of *Cerinthe* are simply single-seeded nutlets which somehow have failed to develop separately during ontogeny. *Cerinthe*, like other genera of the Lithospermeae, no doubt had immediate ancestors with a typical boraginoid fruit consisting of four discrete single-seeded nutlets. In the present genus, the union of the four nutlets into two double nutlets, although presenting a condition suggestive of a primitive one, is actually a late secondary development and accordingly a highly specialized one.

The ovary of *Cerinthe*, viewed shortly after anthesis, is distinctly four-lobed and is generally similar in appearance to that of most Lithospermeae at the same stage of development. The pair of lobes (those derived from one carpel) which will develop into a bilocular nutlet are at this stage united only below the middle, usually for no more than one third their total length. The depth of separation between the lobes within each pair is evidently less than that between the two pairs. Serial transverse sections through the base of the ovary will show the presence of only a basal zone in which the ovarial lobes are united in pairs. Only if in its subsequent development growth is largely confined to this basal zone can the ovary of *Cerinthe* produce bilocular united nutlets. Growth centered above this zone would produce single-seeded nutlets as in other Lithospermeae. In *Cerinthe* growth in the upper zones of the ovary is retarded. The free tips of the ovarial lobes are represented in the mature nutlets only by the bicuspid apex.

The nutlets of *Cerinthe*, when perfectly developed, are two-celled and two-ovulate. Single-seeded one-celled nutlets may be found, but these

always show some evidence of being imperfectly developed. In some unilocular nutlets the undeveloped half may be reduced to a narrow longitudinal ridge, or in others represented only by a discolored spot (i.e., the attachment-scar of the suppressed half) at the base of the nutlet. The attachment scar of the two-seeded nutlet is symmetrical and evenly rounded, but in the one-seeded nutlet it is irregular and somewhat lobed on the side of the nutlet with the suppressed cell. There are other indications that the nutlets of *Cerinthe* are duplex. The tips of the united nutlets remain free when both are equally developed and form the characteristic bicuspid tip to the *Cerinthe* nutlet. The wall separating the two cells within the nutlet is dense and homogeneous. It bears no cavities nor any abscission layer, as frequent in comparable partitions in the nutlets of the Heliotropioideae and the Ehretioideae. The endocarp of the united nutlets is completely confluent. There are, however, lines of suture on the exocarp delimiting the boundaries of the component nutlets. A lineate groove is always present down the middle of the flattened venter, from between the two nutlet-tips down to the base. This groove may also continue more or less clearly down the middle of the convex dorsum and occasionally even be traced across the middle of the attachment scar. In the attachment other evidence of the duplex nature of the nutlet is evident, for the two halves of the nutlet share no vascular supply, both being directly affixed to the gynobase, and each supplied directly from it.

Cerinthe has pollen very different from that of *Onosma* and *Podonosma*, which is surprising, for the corollas and androecium of the three are very similar. The symmetric grains of *Cerinthe* have eight pores borne in a well-marked equatorial groove and associated with eight colpi. The strong equatorial groove distinguishes the pollen from that of all other Lithospermeae. Pollen of *Onosma* and its allies is uniformly three-porate. In number of pores, accordingly, *Cerinthe* is in very much closer agreement with the pollen of *Lithospermum* and its allies and, interestingly, with that of the American genera which most resemble *Onosma* in corolla and androecium. The three natural species-groups within *Cerinthe* have each a distinctive pollen.

The largest grains (33–37 $\times$ 30–33 μ) are associated with the well-marked species, *C. retorta*. These are ellipsoid-sphaeric, almost as broad as long, and possess a narrow equatorial groove and eight linear (not fusiform) colpi which extend well towards the polar areas. The pores are unusually large. In *C. major* L. and its obvious relatives, the pollen grains are barrel-shaped. They are distinctly longer than broad and have convex or nearly parallel sides and abruptly narrowed ends. They measure 24–26 $\times$ 16–18 μ. The grains have a broad equatorial groove and moderately elongate fusiform colpi. The pores are obscure, but apparently always eight in number. *C. minor* L. and *C. glabra* Mill. and their varieties all have similar ellipsoid grains, 18–22 $\times$ 15–18 μ, the smallest in the genus. In lateral profile the sides are convex or slightly angled. The eight pores are associated with an equatorial groove and short fusiform colpi.

14. **Podonosma** Boiss. Diag. ser. 1, 11: 113 (1849) and Fl. Orient. 4: 178 (1875). Type species *Onosma syriacum* Labill.

Plant perennial, herbaceous, or fruticulose at the base, hispid-villose or somewhat hispid with intermixed slender gland-tipped hairs. Stems numerous, simple or laxly branched, loosely spreading or decumbent. Leaves numerous, cauline, lanceolate, acute, with evident midrib, obscurely pinnate-veined or veinless. Cymes loosely scorpioid, borne solitary or geminate, terminal on the stems and leafy branches, in age elongating and becoming unilaterally racemose. Bracts lanceolate, numerous, becoming foliaceous and conspicuous in the fruiting inflorescence. Pedicels slender, elongating in age and usually becoming decurved in fruit. Calyx lobed almost to the base; lobes lanceolate, nearly as long as the corolla-tube, equal or nearly so, in fruit accrescent and becoming lance-cuneate with the tips connivent and the bases reduplicate. Corolla blue, glabrous, regular, inside without faucal appendages or stipitate glands; tube cylindric, abruptly narrowed at the base, without a differentiated throat; lobes narrowly triangular, soon reflexed, twice as long as broad, a quarter to a third the length of the tube, sides straight, apex acute; annulus well developed, villulose, distinctly ten-lobed. Filaments not half the length of the anther, affixed in the upper third of the corolla-tube, compressed, narrowing upward from the base. Anthers elongate, becoming half exserted from the corolla mouth, laterally coherent below the middle, affixed about one fourth of their total length above the base, upper half consisting of a somewhat firm stramineaceous appendage which is narrowed to an acute tip, base emarginate; thecae spreading only at the very base, their lower end with a thickened tip, not coherent; back of anther with a broad slightly prominent stramineaceous connective, not evidently papillate nor muricate. Pollen globose-ovoid, 18–22 × 16–20 μ, broader and more rounded at the lower end; pores three, associated with fusiform colpi, submedial, borne about the broadest part of the grain. Style filiform, tardily exserted from the anther-tube; stigmas united, minute, terminal. Nutlets triangular-ovoid, tuberculate, abruptly bent 90° below the middle, the small substipitate attachment basal on the erect lower third of the nutlet body; ventral keel thick and prominent. Gynobase strongly four-lobed; the lobes pale, cartilaginous, pulvinate, each bearing a small oblique concave attachment surface.

A well-marked genus containing two species, *P. syriacum* (Labill.) Boiss., a plant of cliffs, walls, and other rocky places from Syria to Palestine and east to Iran, and *P. galalense* Boiss., said to be a rhizomatous plant of eastern Egypt. No material of the latter has been seen.

In general habit, glanduliferous herbage, form of calyx, decurved fruiting pedicels, and most important of all, in appearance and structure of nutlets and gynobase, *Podonosma* is extremely similar to *Alkanna* § *Eualkanna*. The corolla and androecium of *Podonosma*, however, is extremely different from that of *Alkanna*. In these floral structures it shows detailed similarities with those of *Onosma*. The similarities with both *Alkanna* and *Onosma* combined in *Podonosma* are so striking and involve so many sig-

nificant details that I am forced to the belief that *Podonosma* shares a close relationship not only with *Alkanna* but also with *Onosma*, one possible only through a shared common ancestry.

The corolla and stamens of *Podonosma* are of the type present in *Onosma*. The most obvious difference in the corolla is in the length of the lobes. In our present genus these are elongate (twice as long as broad) and reflexed, whereas in *Onosma* they are practically always short (about as long as broad) and erect or only loosely recurved. Indeed in only one species of *Onosma*, *O. longilobum* Bunge, are the lobes as elongate as in *Podonosma*. The anthers of *Podonosma*, as in many species of *Onosma*, are united into a tube, but unlike the anthers in the latter genus, those of *Podonosma* cohere only for a limited time and then only along the margin of the fertile lower half, and not at the base of the theca nor along the margin of the terminal appendage. The terminal appendage is conspicuously developed as in *Onosma*, but differs in texture, being pale, firm, straw-colored, and opaque. Unlike that in all species of *Onosma* except *O. longilobum* it narrows to a pointed tip. The back of the anther has a well-developed convex stramineous connective, which, unlike the well-developed connectives in *Onosma*, is not evidently papillate nor muricate.

The pollen is globose-ovoid, 18–22 × 16–20 μ, slightly but distinctly longer than broad and with the lower end more broadly rounded than the upper. The three pores, in furrows, are usually obscure. They are submedial and borne about the broadest part of the grain. This pollen is similar to that in species of *Onosma* which have the anthers united into a tube. It approaches the isodiametric pollen which prevails among the more easterly ranging species of that genus. The pollen of *Alkanna* also has three pores and furrows, but is more elongate and is conic-ovoid rather than globose-ovoid in form.

The nutlets of *Podonosma* are very different from those of *Onosma*, but agree to a remarkable degree with the very unusual nutlets of *Alkanna*, cf. Jour. Arnold Arb. 34: 279 (1953). The nutlets are small, 1–1.5 mm. long, and below the middle are abruptly bent 90° adaxially. The small substipitate attachment scar appears to be superbasally lateral, but morphologically speaking is actually basal on the short section of the nutlet below the bend which remains erect. Dissection of the nutlet reveals that the seed has a transverse flexure across the cotyledons. In situ within the nutlet the tip of the cotyledons is adjacent and vertical to the portion of the pericarp bearing the attachment scar, the proper position in a basifixed nutlet. As in *Alkanna*, but very unlike that in *Onosma*, the gynobase of *Podonosma* bears four pale cartilaginous cushion-like lobes, each bearing a small concave attachment surface on its summit. The attachment surfaces are sloping and the nutlets when affixed to them are accordingly ascending with their tips connivent.

15. **Cystistemon** Balf. f., Proc. Roy. Soc. Edinb. 12: 82 (1883) and Trans. Roy. Soc. Edinb. **31**: 186, t. 56 (1888). Type species *C. socotranus* Balf. f.

15a. **Vaupelia** Brand, Fedde's Repert. **13**: 82 (1914); Green, Kew Bull. **1935**: 528 (1935). Type species *V. barbata* (Vaupel) Brand.

Material adequate for a survey of *Cystistemon* and *Vaupelia* is not available. *Cystistemon* I know only from the original description and illustration. Of the eight species of *Vaupelia* I have only two represented by specimens suitable for analysis, *V. hispida* (Baker & Wright) Brand, from 40 mi. s.w. of Norok, Kenya, *A. G. Curtis 649*, and *V. barbata* (Vaupel) Brand, from betw. Menongue and R. Chimpompo, Angola, *M. A. Pocock 610*. For details concerning the other species of *Vaupelia* I have been forced to rely on original descriptions and upon Brand's synopsis of the genus, Fedde's Repert. **13**: 82–83 (1914).

Cystistemon has a single species endemic to Socotra and *Vaupelia* has eight described species, one in southern Arabia and the others in tropical Africa, where they range from Somaliland to Angola. The two genera are immediately and very closely related and probably should be united. Their affinity with *Onosma* is clear. There seems to be every reason for believing that they represent a southern derivative of that genus in which the corolla-tube has become abbreviated as the corolla-lobes increased greatly in relative size and importance. In all species of *Onosma*, with the single exception of *O. longilobum* Bunge, the tubular portion of the corolla is many times longer than the corolla-lobes. In the present genera the lobes, or at least the well-developed limb, are one to six times as long as the tube, and furthermore are not erect or slightly recurving but spreading. In *Onosma* the throat of the corolla is glabrous or at most only scantily and inconspicuously strigose. It is never villose as in some of the species in the present genera.

The anthers are very conspicuous features in the flowers of *Cystistemon* and *Vaupelia*. They are extremely well developed, much longer than the corolla-tube, and borne on short stout variously modified filaments affixed near the middle of the short corolla-tube, and are accordingly almost completely exserted. The terminal appendage is extremely elongate, and unlike that of *Onosma* usually greatly surpasses the fertile portion of the anther in length. Its tip is usually pointed.

As in some of the species of *Onosma*, the anthers of the present genera are united, but unlike those in *Onosma*, they cohere not at the base and along the sides of the theca but only along the edges of the sterile terminal appendages. The back of the anthers has a prominent broad connective and a papillate surface, as is common in *Onosma*. The base of the anther is more or less emarginate. The lower end of each theca, unlike in *Onosma*, is completely unappendaged or at most has only an inconspicuously thickened tip.

The filaments are of special interest. They are relatively short and stout and affixed to the anther only a short distance above its base. In *V. hispida* they are flattened and ovate-lanceolate in outline and ventrally on their thickened base bear a small triangular ciliate appendage. In *V. barbata* they are narrow but thick and above their base are nearly encircled by a shelf-like ridge ciliate on the margin. Other members of the two genera appear also to have comparable appendages associated with the base of

the filaments. The filaments of *Cystistemon* are described as "obcordatis expansis inflatis basi annulo villoso cinctis." Brand in his diagnosis of *Vaupelia* describes the filaments as "brevia basi andropodio globoso piloso inserta." The hairy appendages associated with the filament in *V. hispida* and *V. barbata* are unparalleled in *Onosma*. If similar structures are associated with the filaments in other members of *Vaupelia*, they provide a character of generic importance. The precise morphological nature of these appendages is uncertain. Those in *V. hispida* and *V. barbata* I found very suggestive of the infrastaminal appendages in *Lobostemon*, cf. Jour. Arnold Arb. 34: 297 (1953). It seems unlikely, however, that the appendages in *Vaupelia* and *Cystistemon* can be homologized with displaced lobes of the annulus as in *Lobostemon*. The annulus is apparently suppressed or absent in *V. barbata*, but in *V. hispida* it is represented at the base of the corolla-tube by ten very minute tufts of hairs. In some species of *Onosma* the lower portion of the filaments may be decidedly hairy, and the base may be decurrent and thickened. Possibly from an ancestral condition of this sort the hairy appendaged base associated with the filaments of modern *Vaupelia* could have been elaborated.

The pollen of *V. hispida* is sphaeric, or in polar profile, sometimes obscurely three-sided. The grains measure 24–26 μ in diameter. The three pores, in furrows, are equatorial. In *V. barbata* the grains are globose-ovoid, as broad as long (20–23 μ) or at most only very slightly longer than broad. In lateral profile the grain is semicircular below the middle, but above the middle it is lightly narrowed and tends to be somewhat flattened at the upper end. The furrows are deep and rather conspicuous. The three pores are slightly inframedial. The pollen, accordingly, is in general agreement with that of *Onosma* and particularly with that of its more eastern species, and especially those with united anthers.

16. **Onosma** L. Sp. Pl. ed. 2, 196 (1762) and Gen. Pl. ed. 6, 76 (1764). Type species *O. echioides* L.

Colsmannia Lehm. Mag. Ges. Naturf. Berlin 8: 92, t. 4 (1818) and Asperif. 2: 356 (1818). Type species *C. flava* Lehm. [= *Onosma sericeum* Willd.].

Perennial or biennial, herbaceous or sometimes fruticulose, coarsely hispid with the hairs either appressed or spreading or frequently strigose or sometimes more or less tomentose, stellate hair-clusters sometimes abundant. Stems erect or spreading, simple or with leafy branches, arising from a taproot or caudex. Leaves with a strong midrib but usually veinless, veins when evident pinnate and usually weak; basal leaves clustered, usually oblanceolate; cauline leaves usually decreasing in size upward along the stem, usually numerous. Inflorescence simple and consisting of single or paired scorpioid cymes terminal on the stem and leafy branches, or a thyrse composed of few to many cymes arising along the stem below the terminal cyme; cymes distinctly scorpioid or loose and the flowers not distinctly biseriate, usually not greatly elongate in fruit. Bracts numerous but conspicuous only in a few species, usually shorter than the adjacent

calyx, sometimes very small and shorter even than the adjacent pedicel. Flowers at anthesis borne on strict pedicels on the curved highest portion of the cyme, held vertically, horizontally or even pendulous according to position on the curve of the cyme. Flowers regular and radially symmetric or in one species with the corolla-bud and the anther-tube strongly curved abaxially. Calyx usually accrescent, lobed to the base or in a few species with a short tube which becomes distended by the ripening fruit; lobes 5, equal or practically so, all distinct or rarely two partially united, very elongate, linear to lanceolate or oblanceolate or ligulate, separated by narrow closed sinus, erect and parallel or in fruit more or less connivent, not imbricate. Pedicels short and stout to slender and elongate, usually lengthening in age. Corolla yellow, blue, or rarely white or red, tubular or obconic-tubular or rarely ellipsoidal, usually gradually enlarging upward from the base or sometimes more strongly ampliate above the middle to form a more or less campanulate throat, usually broadest a short distance below the base of the lobes but sometimes almost cylindric or less commonly broadest at or near the middle, shorter to much longer than the calyx, commonly about twice as long, outer surface glabrous or more commonly evidently puberulent or strigose or hispidulous. Corolla-lobes small, as broad or broader than long (or cuneiform in one species), triangular, acute or with the tip rounded or short-attenuate, erect or with the tip and margins more or less recurved. Corolla-throat without faucal appendages, devoid of glands except those sometimes present about the base of the filaments, glabrous inside or rarely with some appressed hairs along the veins below each corolla-lobe or on and about the bases of the filaments. Annulus usually evident, a well-developed ring or collar, usually more or less lobed and more or less evidently villulose. Filaments affixed below or near or above the middle of the corolla, short to very elongate, shorter to longer than the anther, narrowly ligulate or gradually narrowed upward or sometimes abruptly narrowed above a broadened base, glabrous or rarely hairy or somewhat glanduliferous particularly near the base; base frequently decurrent, symmetric or practically so. Anthers elongate, terminated by a well-developed appendage, usually coherent at the base and frequently joined laterally (usually by interlocking of minute marginal trichomes) to form a tube, usually affixed distinctly below the middle, included in the throat or partially to completely exserted from the corolla; terminal appendage short to very elongate, always evident, strap-shaped or attenuate, hyaline and chartaceous or sometimes firm and somewhat rostrate, tip emarginate or sagittate or sometimes obtuse, but rarely acute; thecae distinct and usually spreading for a short distance above their appendaged base, or rarely joined and parallel throughout and their basal appendages broadly joined and making a subtruncate or emarginate base to the anther; basal appendage usually short and thick, sometimes hardly more than a distinctly thickened basal tip of the theca, those of adjacent anthers usually coherent but those on the same anther usually distinct. Pollen usually sphaeric to ovoid and as long or longer than broad, 16–25 × 16–23 μ, but in one species strongly oblate, transversely elliptic and measuring

13–14 × 16 μ; polar profile circular or more or less three-sided; pores three, associated with fusiform furrows, equatorial to suprabasal. Style filiform, glabrous or very rarely hairy, usually becoming exserted from the corolla and surpassing the anthers, commonly emerging from the corolla as the bud unfolds but sometimes emerging precociously from corolla-buds which have not yet attained maximum size and in species with united anthers sometimes very tardily emerging from the synandrium, usually persisting until the fruit is ripened; stigmas two, distinct or partially to completely united, usually juxtaposed and terminal on the style, rarely subterminal and separated by the very short obtusish sterile tip of the style. Nutlets erect, small to large, smooth or less commonly variously tumulose or verrucose or rugose, lustrous to opaque, gray to olivaceous brown or blackish, frequently mottled, never white, somewhat ovoid to broadly lanceolate, frequently somewhat rostrate and in one species with terminal and lateral cornute appendages; venter usually angled, rarely with a thickened ventral keel; dorsum convex or sometimes flattened below the middle; ventral suture fused and obscure; attachment scar basal, usually triangular, as broad as long, horizontal or somewhat oblique, sometimes green. Gynobase pyramidal or flat or even depressed at the center, the attachment faces usually distinct, frequently concave.

A large and variable genus with species occurring from northwest Africa and Middle Europe east to southern Siberia and to western China and Burma. Stroh, Beiheft Bot. Centralbl. **59B**: 430–454 (1939) in a recent purely bibliographic listing of the species, enumerates 123 species referable to the genus as here accepted. Subsequent to Stroh's census *O. sericeum* and its allies have been treated by Levin, Not. Syst. Leningrad 12: 228–41 (1950), and Popov has published a detailed discussion of the genus, Proalemy botaniki 1: 70–108 (1950) and also, Not. Syst. Leningrad 14: 287–304 (1951) a key in Latin as well as in Russian covering the thirty-four species accredited to the U.S.S.R. The twenty-nine Chinese and Indian species have been keyed and described by Johnston, Jour. Arnold Arb. 32: 201–356 (1951).

The genus has its closest relatives in *Maharanga*, *Vaupelia*, *Cystistemon*, and *Podonosma*. Other close relations within the Lithospermeae are with *Alkanna*, *Echium*, and *Cerinthe*. American genera, such as *Onosmodium* and *Lasiarrhenum*, sometimes suggested as relatives of *Onosma*, appear to be more closely related to *Lithospermum* and are mimics of *Onosma* rather than close relatives of it.

The corolla is almost always coarsely tubular, from the base moderately and gradually expanding for most of its length or becoming more abruptly expanded near the middle and differentiated into a stout tube and a more or less campanulate throat. Such corollas are broadest a short distance below the base of the small, commonly deltoid lobes. A noteworthy departure from such conventional forms occurs in a few species. In *O. pyramidale* Hook. of the Himalayas, the corolla has an abbreviated proper tube and a large inflated throat. It is ellipsoid in form and hence suggestive of the corollas of *Maharanga*. In *O. stenosiphon* Boiss. of Iran, the

corolla is scarcely at all ampliate, being very elongate and slenderly cylindrical. The most aberrant corolla is that of *O. longilobum* Bunge, of northeastern Iran and adjacent U.S.S.R., the only member of the genus with the lobes conspicuously longer than broad. It has a gradually ampliate tube and throat, together ca. 4 mm. long, and is broadest a short distance below the base of the lobes. The erect lobes, cuneate with an attenuate tip, are 2 mm. wide at the base and about 6 mm. long, and hence longer than the tubular portion of the corolla. They are loosely folded longitudinally (conduplicate) and the throat below them is angulate. The tube has five elongate invaginations, one below each filament attachment. Inside, the corolla is orthodox except for the terminal appendage of the anthers, which gradually taper to a slender point. Because the corolla of *O. longiloba* is so aberrant, it is probably inevitable that sooner or later the species will be given generic recognition. I have refrained from doing so because the plant, in all details other than corolla-form and pollen, is remarkably similar to *O. stenosiphon* Boiss. and *O. limitaneum* Johnston and apparently closely related to them. To be sure, these two latter species are not conventional members of *Onosma*, for both have small, unusually slender and elongate corollas, and *O. limitaneum* has somewhat tailed anthers and usually rounded, rather than deltoid corolla-lobes. They are, however, readily accommodated in *Onosma*, and *O. longilobum*, because of its relations with them, even though its corolla is aberrant, can be accommodated in the genus also.

The species of *Onosma* usually have corollas with perfect radial symmetry. Indeed, the only notable departure from this condition is that previously reported in Jour. Arnold Arb. 32: 223 (1951) in *O. multiramosum* Hand.-Mazz. of China. In that species the corolla-buds and the anther-tube are both conspicuously bent abaxially above the middle. Though other species with slender corolla-buds may have an occasional bud showing a slight subapical bend, in none of these is it so consistent and extreme as in *O. multiramosa*. In the closely related *Maharanga* the filament-bases within each corolla are clearly differentiated into three types, and in this respect the androecium has a manifest bilateral symmetry. This is not so in *Onosma*. In the vast majority of species in *Onosma* the stamens within the corolla are indistinguishable. If differentiation of the filaments does exist in *Onosma*, as perhaps very obscurely in *O. Waddellii* Duthie, *O. Wardii* Johnston, and *O. mertensioides* Johnston, the difference is very slight and difficult to detect.

Among the most distinctive features of *Onosma* are its elongate anthers. These are almost always coherent, at least at the base, and are always terminated by an evident sterile appendage. Descriptions of the organ by past authors seem to have been largely if not exclusively based upon its representation in the species of Europe and the Near East. Among the Chinese, Indian, and some of the species of the Middle East, the organ shows more variation than is generally recognized. In western species the anthers, if joined, are coherent only at the base, but in many of the more eastern species they unite laterally to form a tubular synandrium. Simi-

larly, western species have a terminal appendage that is strap-shaped and papery hyaline, whereas among the more easterly ones the appendage on the anther is frequently much firmer in texture, dark in color, more attenuate, and frequently somewhat rostrate in nature. Among the western plants the anther averages very much larger than in the east. The connective on the back of the anther, conspicuously developed and usually broad and prominent in the west, becomes very narrow and inconspicuous in many of the eastern species. The back side of the anther usually has its surface papillate or muriculate. Among eastern species, however, it may be nearly smooth. In most all species the anther has its thecae distinct and more or less evidently spreading for a short distance above the base, and the lower end of each theca is thickened and more or less prolonged to form a short basal appendage. Only in *O. limitaneum* are the appendages notably elongate. In *O. multiramosum* and to a less extent among other Chinese species, the thecae remain joined and parallel for their total length, and their broadened and confluent basal appendages form a truncate or weakly emarginate base to the anther.

Pollen of forty-five species of *Onosma* has been examined. The grains have three pores which are frequently somewhat protrudent and are always associated with fusiform colpi. In polar profile the grains may be circular or more or less three-sided with the angles rounded or emarginate. The pollen varies from species to species in lateral profile. All the many intermediate forms between decidedly ovate and perfectly circular and even transversely elliptic are represented. The lateral outline, as in *O. echioides* L., *O. arenarium* W. & K., and *O. dichroanthum* Boiss., can be decidedly ovate with the length evidently much greater than the breadth (25 × 16–20 μ). In such grains the pores are borne where the grain is broadest, about a third of the length of the grain above its base. In other species the grains may still retain a modified ovate outline but show less difference between length and breadth. In *O. confertum* W. W. Sm., for example, the grains are equal or practically so in length and breadth (16 μ) but are noticeably more broadly rounded below the inframedial pores than above them. From grains such as these there are many transitions to grains with equatorial pores and equal hemispheres, in which the lateral profile is perfectly circular or even very slightly broader than long. In *O. pyramidale* Hook. the grains have a polar axis which is obviously shorter than the breadth at the equator (13–14 × 16 μ). In lateral profile these grains are distinctly transverse-elliptic. The pores are equatorial or at most only very slightly inframedial.

Most of the species of Europe and the Near and Middle East have pollen of the ovoid type, i.e., longer than broad, 20–25 × 16–20 μ, and bearing the pores well below the middle, usually ca. 8 μ above the base of the grain. Among the Sino-Indian species, only seven out of the twenty-nine species have pollen of this type, viz., *O. chitralicum* Johnston, *O. hispidum* Wall., *O. khyberianum* Johnston, *O. barbigerum* Johnston, *O. Griffithii* Vatke, *O. bracteatum* Wall., and *O. dichroanthum* Boiss. Species with grains isodiametric or nearly so (16–26 μ) are most abundant in the

more eastern portions of the range of the genus. There are twenty-two of the twenty-nine Sino-Indian species with pollen of this type. Among the species of the middle East I have encountered the type only in species such as *O. stenosiphon* Boiss. and *O. rostellatum*, which appear to be more closely related to the Indian and Chinese congeners than to the conventional Onosmas of Europe and the Near East. Interestingly, similar pollen occurs in *Vaupelia*, a very close relative of *Onosma*, which has long-exserted united anthers, as do many of the eastern species of *Onosma*.

17. **Maharanga** A.DC. Prodr. **10**: 71 (1846). Type species *Onosma Emodi* Wall.

Plants herbaceous, perennial or biennial or perhaps sometimes annual. Stems one to several, erect to decumbent, hispid or hispid-villose, simple or with strict to ascending leafy floriferous branches, arising from a cluster of basal leaves or more commonly from among the remnants of a leaf cluster produced the previous season. Leaves very obscurely to evidently veined; veins strictly ascending, usually pinnate but frequently with the lowest pair most elongate and most prominent; basal leaves usually oblanceolate; cauline leaves numerous, the middle and upper ones usually larger than those near the base of the stem, oblanceolate to lanceolate, usually hispid or hispid-villose with the hairs frequently appressed, hairs scanty to abundant and those on the upper leaf-face frequently with discoid bases, stellate hair-clusters present in two species. Cymes usually geminate, not clearly scorpioid and forming somewhat glomerate clusters broader than long, terminal on the main stem and sometimes also on the leafy branches, in fruit loosening to become somewhat corymbose or rarely loosely racemose. Bracts small, narrow, not conspicuous, none except the lowermost surpassing the adjacent calyx. Calyx with a broad deeply saucer-shaped or shallowly cup-shaped tube and ascending lobes; lobes cuneate or narrowly triangular, gradually narrowed from a broad base, one and a half to three times as long as broad, separated by open angulate sinus, tip acute or somewhat attenuate; lobes in fruit becoming loosely incurved and the two abaxial ones sometimes slightly larger than the other three; pedicels elongating, in fruit usually slender and as long or longer than the calyx. Corolla blue, purplish, yellow or white, about twice the length of the calyx, outside strigulose or villose-hispidulous, ovoid-ellipsoid or obovoid, contracted at both ends, abruptly expanding from a short tube into a relatively large inflated throat and at or above the middle contracting to a small mouth, above the middle usually with persisting narrow inflexed vertical plaits and hence appearing sulcate below each sinus, below each lobe with an inflated rib that protrudes between the calyx-lobes and has an abruptly contracted lower end that rests chin-like in the broad angulate sinus between the calyx-lobes, outside below the middle and usually hidden by the calyx-lobes bearing five elliptical glabrous areoles which are usually slightly depressed and sometimes invaginate near their upper end; mouth of corolla very small; lobes very small, more or less deltoid, loosely recurved above the middle, as long as broad or somewhat

longer than broad, apex acute or rounded; inside of corolla glabrous or more or less hairy about the bases of the filaments, devoid of glands or faucal appendages; annulus evident, collar-like, more or less villulose. Filaments affixed at base of the throat, abruptly narrowed from a broad base, slightly longer than the anthers or distinctly shorter, two filaments with a symmetric base, a medial vein and a transverse attachment on the corolla, the other three with an oblique or vertical attachment and an asymmetric base with an excentric vein. Anthers lanceolate, always included, coherent at the base, affixed below the middle, terminated by a usually well developed, firm, gradually attenuate sterile appendage which is usually armed with some stout ascending hairs or cuneiform teeth on the margin and by a cluster of cuneiform teeth at the apex, base of anther with the thecae distinct and somewhat spreading; back of anther very obscurely papillate, the connective narrow and neither prominent nor conspicuous. Pollen cylindric or in one species ellipsoidal, pores three, equatorial, associated with fusiform colpi; polar profile circular or three-sided with notches at the corners. Style filiform, glabrous, included or short exserted, rarely persisting with the fruit; stigmas two, juxtaposed and terminal on the style, small, distinct or more or less united. Nutlets slightly incurved, brown or olivaceous, dull, tumulose and coarsely rugose with the surface very abundantly and densely muriculate or papillate, somewhat ovoid, with the venter angulate and provided with a coarse prominent ventral keel; ventral suture absent; attachment scar basal, about as broad as long. Gynobase broadly pyramidal, the sloping attachment surfaces separated by low cartilaginous ridges.

A group of nine species occurring in the mountains from the middle Himalaya east into southwestern China. The genus is obviously related to *Onosma* but is readily distinguishable by its calyx and pollen, as well as by the form and structure of its corolla.

The corolla of *Maharanga* has a very short proper tube and a relatively large, well-developed, much inflated throat, usually broadest near the middle. The mouth of the corolla and the base of the tube usually have about the same diameter. In *Onosma* the corolla form of *Maharanga* is closely simulated only by the inflated ellipsoid corolla of *O. pyramidale* Hook. This lacks, however, the characteristic outward features of the corolla of *Maharanga*, such as the narrow, tightly inflexed plaits below each sinus and, below each corolla-lobe, the distinctly puffed-out ribs which have an abruptly contracted lower end that rests chin-like in the angle of the open sinus between the calyx-lobes. Also lacking in *Onosma pyramidale* is the glabrous elliptical areole on the outside of the corolla which is associated with the very different attachment of the filaments in *Maharanga*.

The filaments are abruptly narrowed and become more or less linear above their broad base. They are affixed directly on the corolla-walls or arise from the shoulders of gibbose invaginations. The five stamens within the corolla differ in the shape of the filament, in the course of the vein within them, and in the orientation of their attachment on the corolla-

walls. Two filaments have an arcuate attachment oriented transversely, and their vein is medial. Two other filaments are obliquely affixed, and their asymmetric base has an excentric vein. The fifth stamen (apparently the medial adaxial one) is vertically affixed and has a strongly excentric vein and a more prolonged and asymmetric decurrent base. Although no evidence of it has been detected elsewhere in the corolla, bilateral rather than radial symmetry is manifest in the filaments of *Maharanga*. In *Onosma* the stamens are all similar, or if there is any differentiation among them within the corolla it is very obscure.

The anthers of *Maharanga* in size and general form are similar to those in some species of *Onosma* (e.g., *O. pyramidale* Hook. and *O. cingulatum* W. W. Sm.) but differ from those of most species of that genus in their smaller size, narrow smoother connective, and firmer dark, beak-like terminal appendage. Occasionally in *Onosma* as in the species just mentioned, the terminal appendage of the anther may be obscurely papillate on the margin and so appear very minutely denticulate. In all species of *Maharanga*, except *M. bicolor* DC., the lateral margins of the appendage bear some short, stout, ascending hairs or subulate teeth. The tip of the appendage in *Onosma* may be attenuate, truncate, emarginate, or bidentate. In *Maharanga* the very tip appears to be somewhat thickened and commonly bears a number of cuneiform teeth, sometimes in a more or less crown-like arrangement.

The pollen of *Maharanga* is 3-porate and 3-colpate as in *Onosma* but is very different from that of *Onosma* in form. The grains (20–23 × 10–16 μ) are elongate and in most species are cylindric. In lateral profile they have abruptly rounded ends and sides that are nearly straight and parallel except for a weak constriction at the equator. The pores are equatorial. In polar profile the grains are circular or somewhat three-sided with the broad corners somewhat emarginate. The only departure from the cylindric form described occurs in *M. bicolor*. In that species, aberrant in a number of other minor details (included style, relatively large united stigmas, and very elongate laterally unarmed anther appendages), the pollen grains are distinctly ellipsoid. In lateral profile the sides are rounded or slightly angled at the equator where they are broadest and bear the pores.

The nutlets of *Maharanga* are similar in size and form to those of many of the Chinese species of *Onosma*, and like many of the latter they have a rough, tumulose, and rugose epicarp. The distinctive feature of the *Maharanga* nutlet is the surface of the epidermis, which is very abundantly and very densely beset with crowded minute papillae or muriculations. Only in a very few Chinese and Indian species of *Onosma* are the nutlets provided with comparable minute epidermal roughenings, and even in these they are never so well developed and so very abundant as on the nutlets of *Maharanga*.

The units of the inflorescence are not of the extreme scorpioid type prevalent among the species of *Onosma*. In *Maharanga* the rhachis of the cyme remains relatively slender and is not greatly elongate. The flowers, neither extremely numerous nor evidently biseriate, become slenderly ped-

icellate. Cymes resembling those of *Maharanga*, however, are developed in some Chinese species of *Onosma* such as *O. album* W. W. Sm., *O. confertum* W. W. Sm., *O. cingulatum* W. W. Sm., *O. exsertum* Hemsl., *O. fistulosum* Johnston, and *O. paniculatum* Bur. & Franch., as well as in such congeners from the Middle East as *O. stenosiphon* Boiss., *O. longilobum* Bunge, and *O. polyphyllum* Ledeb.

The species of *Maharanga* have been described and distinguished, as members of the genus *Onosma*, in my treatment of the "Sino-Indian Species of Onosma," Jour. Arnold Arb. 32: 206, 356–67 (1951). With the validity of the genus *Maharanga* now recognized, the following new binomials are required:

Maharanga verruculosa (Johnston), comb. nov.

Onosma verruculosum Johnston, Jour. Arnold Arb. **32**: 356 (1951).

Maharanga Borii (Fischer), comb. nov.

Onosma Borii Fischer, Kew Bull. **1940**: 38 (1940).

Maharanga lycopsioides (Fischer), comb. nov.

Onosma lycopsioides Fischer, Kew Bull. **1940**: 39 (1940).

Maharanga microstoma (Johnston), comb. nov.

Onosma microstoma Johnston, Jour. Arnold Arb. **32**: 360 (1951).

Maharanga dumetorum (Johnston), comb. nov.

Onosma dumetorum Johnston, Jour. Arnold Arb. **32**: 361 (1951).

Maharanga egregia (Johnston), comb. nov.

Onosma egregium Johnston, Jour. Arnold Arb. **32**: 366 (1951).

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SOME DETAILS OF THE STRUCTURE OF RHODOTHAMNUS CHAMAECISTUS

HERBERT F. COPELAND

With one plate

THIS NOTE is a supplement to my paper (1943) on the genera of the subfamily Rhododendroideae of the family Ericaceae. In that paper, the genus *Kalmiopsis* Rehder (1932) was suppressed: its only species, *K. Leachiana* (Henderson) Rehder, an undershrub local on certain summits in southwestern Oregon, was transferred to *Rhodothamnus*. This was done without original study of the only previously recognized species of *Rhodothamnus*. The latter, *R. Chamaecistus* (L.) Reichenbach, is local on the Alps; under the conditions of the times, it had been impossible to obtain material of it. As soon as communication between Germany and America again became feasible, Dr. Hermann Sleumer had the kindness to send material of *R. Chamaecistus* fixed for histological study. The material is from cultivated plants *ex Museo botanico Berolinensi*, and was collected during and just after flowering, in April and May, 1948. It has been subjected to the remaining steps of routine microtechnique and duly studied. The results permit further discussion of relationships between *Kalmiopsis* and *Rhodothamnus*.

Rhodothamnus Chamaecistus is an undershrub with crowded small thick alternate leaves. In spring, it produces a few flowers on long pedicels arising from between pairs of bracteoles in the axils of leaves near the tip of the stem. The growth of the vegetative shoots of the year, terminal and axillary, begins at about the same time.

The flowers (*fig. b*) have five narrowly triangular sepals; a pink corolla with a brief tube and a rotate limb, 5-lobed, with deep sinuses; ten long-exserted stamens; a depressed-globular ovary with five locules opposite the lobes of the corolla; and a long style springing from a depression in the summit of the ovary, the stigma not expanded. The flower is slightly zygomorphic; the median petal is on the lower or abaxial side. The sepalad stamens are of greater average length than the petalad stamens, the longest stamens of both whorls being on the adaxial side. The anthers (*fig. c*) are elongate. The two terminal "pores" of each anther are actually brief slits which gape widely at maturity.

The leaves, but not the bracteoles, are ciliate with stout gland-tipped bristles. Stems, pedicels, and calyces are beset with similar bristles. There are simple hairs on stems, pedicels, ovaries, and the bases of the filaments.

The stems are of the same internal structure as those of other Rhododendroideae, being of the type which lack a cylinder of fibers of pericycle.

The leaves reach a width of about 3 mm. and are about 300 μ thick

(*fig. a*). The epidermis is of large cells with a thick cuticle; the cells are larger, and the cuticle is thicker, on the upper side. The stomata are confined to the lower epidermis and open at the level of the outer surface. The guard cells bear a ridge at the outer opening of the stomatal passage, but not at the inner opening. There are two or three layers of palisade cells occupying about half of the thickness of the leaf. The veins are not joined to the epidermis by flanges of differentiated tissue; they are imbedded between palisade and spongy tissue. Each vein contains a conspicuous strand of fibers between the xylem and phloem.

The base of the floral receptacle is impressed. The ten main perianth bundles which arise from the stele in this region (*fig. d*) are recurved at their origin. Theoretically, these bundles are two whorls, but all arise at approximately the same level. Five of them are the median bundles of sepals. The five which alternate with these undergo forking, each into three; the middle branch forks again and supplies a lobe of the corolla; the lateral branches are the lateral bundles of the adjacent sepals. There are occasional deviations from the typical pattern thus described. The ten stamen bundles arise from the upper sides of the main perianth bundles. The vascular tissue which continues beyond the departure of the main perianth bundles forms for the most part five bundles, fused pairs of ventral bundles of adjacent carpels, which ascend the central column of the ovary in the planes of the septa to about half the height of the ovary. Each of them divides into two branches which run out into placentae in adjacent locules. From the bases of the perianth bundles and the carpel ventrals small bundles originate, in no evident pattern, and run out into the ovary wall. Some distance above the base of the ovary, five of these small bundles become recognizable, by their course in the median planes of the carpels, as carpel dorsals. The other small bundles fade out; the carpel dorsals ascend the ovary wall to its summit, dip under the depression about the base of the ovary, and ascend the style.

The internal structure of the ovary, the moderately elongate ovule (*fig. e*), and the embryo sac are quite as in other Rhododendroideae.

Nearly all of the observed characters of *Rhodothamnus Chamaecistus* are those which are to be expected of a plant included in subfamily Rhododendroideae and tribe Phyllodoceae. Zygomorphy is somewhat more evident in the flowers of this plant than in those of other members of the tribe, and the rotate corolla with deep sinuses is exceptional. The anthers and the vascular system in the receptacle are quite as in *Kalmiopsis Leachiana, Kalmia*, and *Phyllodoce*. The anatomy of the leaves is essentially exactly as in *Kalmiopsis Leachiana*: Breitfeld (1888) was mistaken (so far as the available material shows) in describing the epidermal cells as small and the veins as "*durchgehend*." *Kalmiopsis Leachiana* remains different from *Rhodothamnus Chamaecistus* in its larger leaves, its more extensive inflorescence, its shallowly indented campanulate corolla, and particularly in its peculiar scales, which simulate those of *Rhododendron* and *Ledum* while not being of the same structure.

Judgment as to the expedient limits of taxonomic groups is often in-

escapably subjective. To such judgment it appears, more definitely than before, that *Kalmiopsis* is not to be maintained as a genus. The plant of southwestern Oregon is to be called *Rhodothamnus Leachianus*. As represented by the two species here ascribed to it, *Rhodothamnus* is indeed a remarkable example of interrupted distribution.

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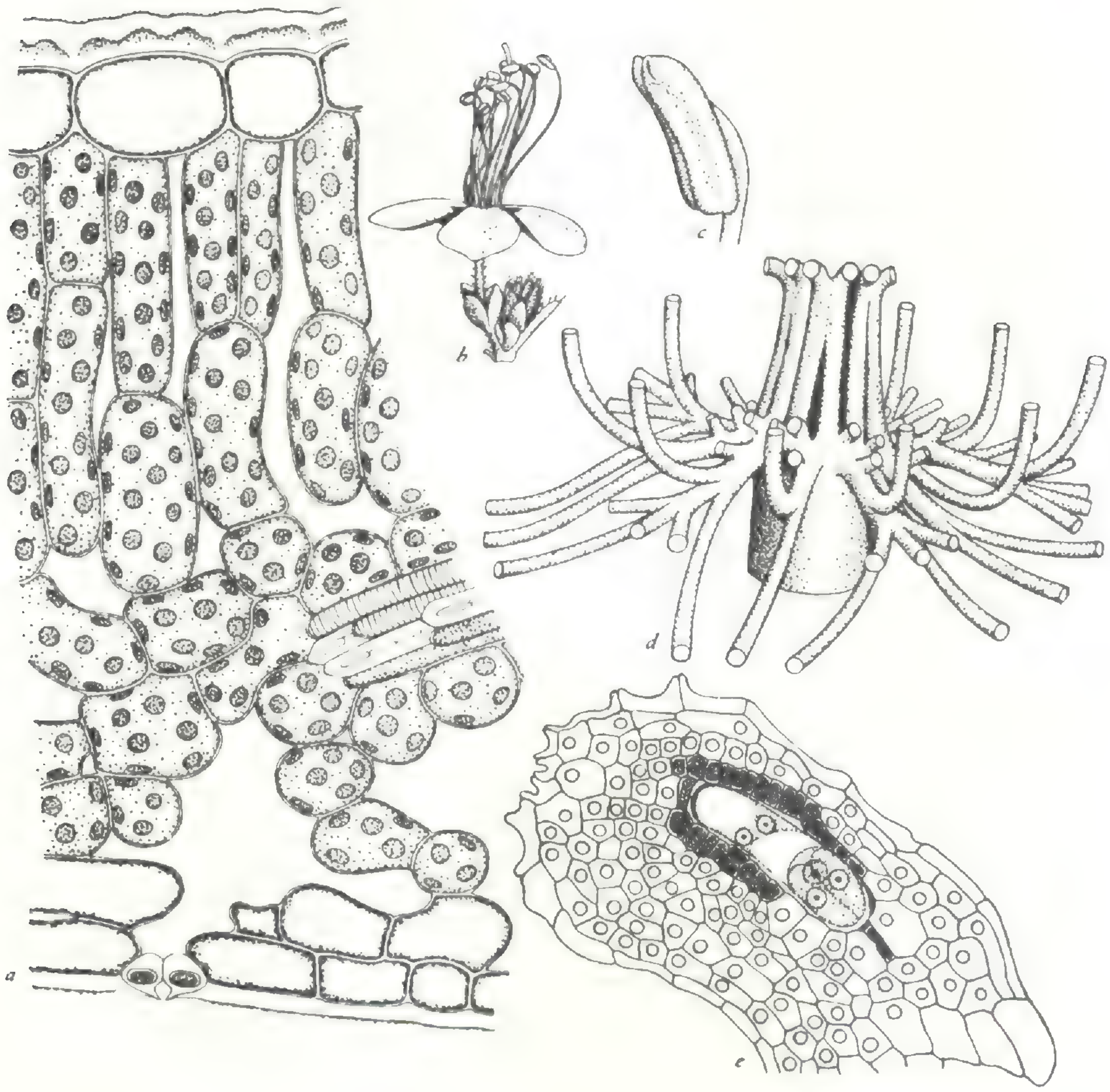

RHODOTHAMNUS CHAMAECISTUS (L.) Reichenbach

RHODOTHAMNUS CHAMAECISTUS. a, cross section of leaf × 320. b, flower × 1.6. c, anther × 8. d, vascular system in the floral receptacle × 40. e, ovule × 320.

TWO NOMENCLATURAL CHANGES IN THE CHINESE FLORA

ALBERT N. STEWARD

DURING THE STUDY of herbarium specimens and literature related to the flora of the Lower Yangtze Valley it has come to the attention of the writer that there is confusion in the nomenclature of the species described by Hemsley under the name *Diospyros sinensis* in Jour. Linn. Soc. Bot. 26: 71 (1889).

It appears that this name was earlier ascribed by Naudin to Blume in Nouv. Arch. Mus. Paris II. 3: 221 (1880) to cover what is probably a form of *D. Kaki*, since Naudin cites *D. Roxburghii* (Carr. Rev. Hort. 1872, p. 253, *fig. 28–29*) as a synonym of *D. sinensis*, and the figures for *D. Roxburghii* appear very much like a form of *D. Kaki*. Perhaps Naudin had in mind Blume's *D. chinensis* (Cat. Gewass. in 's lands Plantentuin te Buitenzorg, p. 110. 1823), which is a synonym for *D. Kaki* Linn. The name now proposed for this species is:

Diospyros cathayensis nom. nov.

Diospyros sinensis Hemsl. in Jour. Linn. Soc. Bot. **26**: 71 (1889), non Blume ex Naudin in Nouv. Arch. Mus. Paris II. 3: 221 (1880).

This wild persimmon was well described by Hemsley in Index Florae Sinensis (cited above) and was later figured in Hooker's Icones Plantarum 29: *t. 2804* (1906). It was reported by Rehder and Wilson as "a common small evergreen or subevergreen tree in the dry valleys of western Szechuan" in Pl. Wils. 2: 591 (1916). The type specimen was collected by Faber at an elevation of 4000 ft. on Mt. Omei, Szechuan. In addition to other localities in Szechuan, the species is now known from stations in Hupeh and Yunnan in Western China, and from Chekiang, Kiangsi, Fukien and Kwangtung in Central and Southern China.

Desiring to follow a conservative procedure as to nomenclature in connection with studies on the flora of the Lower Yangtze Valley, it has seemed best to use *Satureja* Linn. in the broad sense and not to treat *Calamintha* Lam. as a separate genus. Consequently, the following combination becomes necessary:

Satureja polycephala (Vaniot) comb. nov.

Calamintha polycephala Vaniot in Bull. Acad. Géogr. Bot. **14**: 183 (1904).

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STUDIES IN THE KUHNIINAE (EUPATORIEAE) II *

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With five plates

INTRODUCTION

Liatris and *Brickellia*, the two largest genera of a small subtribe of the *Eupatorieae*, which Robinson (1913) called the *Kuhniinae*, were examined cytologically and found to have the basic chromosome numbers of 10 and 9 respectively. *Brickellia* with approximately ninety species (Robinson 1917) has its greatest distribution in Mexico and southwestern United States. It extends northward to the Canadian border and southward into Central America and sparingly into Brazil. The range of *Liatris*, with thirty-two species (Gaiser 1946), is confined almost entirely to southern Canada and the United States, though it just crosses the border into Mexico. The remaining seven genera are small. However, their distribution in the American hemisphere is interesting in relation to the two large genera mentioned. *Barroetea* is wholly Mexican and *Kanimia* is found only in South America. Two others, *Trilisa* and *Carphephorus* occur only in southeastern United States while the monotypic genus *Garberia* is limited to Florida. Only the two genera, *Kuhnia* and *Carphochaete* overlap from United States into Mexico.

The comparative growth-form of these genera is also a matter of interest. *Liatris* is a genus of perennial herbs with mostly corm-like rootstocks, though in the series *Punctatae*, deeply penetrating roots occur, and the singular *L. Garberi* of the *Spicatae*, has a tuberous form. By contrast, *Brickellia* consists largely of shrubs or shrubby perennials, of which probably the most woody is *B. argyrolepis*, which attains a height of twelve feet and a stem diameter of two inches (Gaiser 1953). It is difficult to sharply differentiate between herbs and shrubs in this genus, for the stem is often only slightly woody at the base or consists of a woody caudex. Others are perennial herbs with only persistent underground parts which are fusiform, tuberous or more knobby and rhizomatous. Only one species, or possibly two, are annuals. Of the seven species of *Barroetea* (Robinson

* Chromosome Studies in the Kuhniinae (Eupatorieae). I. Brickellia. Rhodora **55:** 253–267, 269–288, 297–321, 328–345 (1953).

1911b), one is known to be a perennial herb, somewhat woody at the base, and three are recognized as annuals. *Kuhnia* species are comparatively slender herbs with long somewhat conical roots which have been described by Shinners (1946) as irregularly divided at the top and becoming more or less "soft-woody." Robinson (1911a) described *K. adenolepis* as having a woody caudex. *Carphephorus* and *Trilisa* are true perennial herbs having clustered, thick, almost tuberous roots and leafy rosettes. The single species of *Garberia* is definitely a woody shrub attaining a height of six to eight feet, while the species of *Carphochaete* are generally spoken of as small branching shrubs.

In the cytological studies of *Liatris*, including all the given species except *L. lancifolia*, only the diploid number (2n = 20) was found in those of nine series, while polyploidy prevailed in the *Punctatae* (Gaiser 1949, 1950, 1951). In one species only the hexaploid number was found, in a second, only the tetraploid, in a third, the diploid, while both diploid and tetraploid numbers occurred in two others. Further, one of these two latter, *L. punctata* Hook. has the widest distribution of any species in the genus, extending the full north-south range from western Canada, east of the Rocky Mountains, over the Mexican border. In forty-one species of *Brickellia* examined, representing half of the undoubtedly distinct species, and four sections, only the diploid number (2n = 18) was found.

On the basis of previous cytological work, it seemed worth while to determine [1] the chromosome numbers in the other genera of this small group of the *Compositae* with the hope that new clues of relationship would become evident. From fossil evidence, the family is believed to be of recent development. With the two largest genera known to differ by one in their chromosome number, questions arose: Was there a smaller basic number? If so would it be found in genera limited to the tropics or to the more woody forms? Would those that were shrubby have the same number as *Brickellia* and the perennial herbs the same as *Liatris*? Or would there be still further variations in number and if so what relationship would this bear to the classification?

There was also the interesting problem of polyploidy, since though lacking in *Brickellia*, it was found in *Liatris*, a genus limited to the temperate zone. There have been contributions which fail to confirm but also some which give support to Hägerup's original hypothesis (1932) that polyploidy developed under rigorous environmental conditions. In Stebbins' (1950) discussion on the topic of the polyploid complex and geographic distribution he stated that no tropical group was known well enough to be included. When undertaking the study of *Brickellia*, it was expected that because of its range into Mexico and Central America it

[1] The author gratefully acknowledges a grant from the Canadian Research Council when a beginning was made. Subsequently the project was assisted by a grant from the American Philosophical Society which permitted the collection of species of *Barroetea* and *Kuhnia* as well as *Brickellia* in Mexico, without which this investigation could not have been completed.

would include tropical forms. Field experience in the collection of approximately two dozen species from Mexico and Guatemala impressed upon the author that they were on the plateaus and thus were actually existing in a temperate climate. The annual *B. diffusa* is somewhat exceptional for although it occurs on the plateaus too, it is the only species to be found throughout the Caribbean. All of the species of *Barroetea*, according to Robinson (l.c.) occur on the plateaus in Mexico, and no species has penetrated northward beyond its central zone. There is no monograph of *Kanimia* but the labels on specimens at the Gray Herbarium indicate that they have come from regions in the Andes from the Colombian border to Peru and the province of Minas Gerais, Brazil. Thus there are not included in this subtribe, plants of tropical lowlands such as make up the genus *Anthurium* of the *Araceae*. But we know that polyploidy does appear in five of a total of thirty-nine species of that genus examined (Gaiser 1927). Stebbins (1950) apparently overlooked this when he made the statement cited above. In contrast to one large tropical genus, as *Anthurium*, the *Kuhniinae* present a challenging succession of related forms which appear to have progressed northward from the tropics in varying degrees.

NOTES ON THE TAXONOMY OF THE GENERA

In his key to the *Eupatorieae*, Robinson (1913) added an additional subtribe to those given by Hoffmann (1890), and changed the name of the *Adenostylinae* to *Kuhniinae* because the assumed type genus *Adenostyles* did not really belong to the tribe. With its omission from this subtribe, the other nine genera remain the same.

Of them the genus *Kanimia* stands alone in having a definite number of phyllaries. Both in the number of florets and phyllaries it is like *Mikania*, from which Hoffmann (l.c.) had stated it was only separated by its 8–10 ribbed achene. However, *Mikania* is placed at the end of the previous subtribe *Ageratinae*. There is no general treatment of *Kanimia*. Thirteen species have been described from Colombia, Peru, Ecuador, and Brazil. Because it is South American, consists largely of vines or woody forms, as are included in the much larger genus *Mikania* and has a definite number of florets and phyllaries, a strong link is suggested between the two subtribes. Whether the chromosome number would be of any help in adjustment of generic segregation, will have to await the procuring of cytological materials of *Kanimia*.

It is a matter of great satisfaction that of the remainder, the four largest genera had been monographed, and two of them by Robinson, whose specialty was the *Eupatorieae*. Thus we have the excellent treatment of *Brickellia* in 1917, following that of *Barroetea* in 1911, and the key to the whole group in 1913. The genus *Kuhnia* was dealt with by Shinners in 1946, as had been one series of the genus *Liatris*, the *Scariosae*, in 1943. The latter genus was in the process of being revised by Gaiser at that time and publication followed in 1946. Of the four other genera still

lacking comprehensive treatments, a brief summation of their status is given here.

Carphochaete

Next to the singular *Kanimia*, *Carphochaete* stands apart from the rest of these genera in the nature of its pappus, which is scale-like and dilated at the base, instead of being setose.

There has been no recent treatment of this genus, which was established by Gray (Pl. Fendl. 65, 1849). It was based on a somewhat shrubby herb from northern Mexico, and named *C. Wislizeni* for its collector. In 1852, Gray (Pl. Wright. 89) emended the description of the genus as shrubby or herbaceous but shrubby at the base, when describing two new species, one Mexican, *C. Grahami*, and the other from the boundary region of Mexico and New Mexico, *C. Bigelovii*. Since then only one other species has been added by Greenman (Proc. Am. Acad. Arts & Sci. 44: 34, 1904). It also is Mexican and was considered as an herbaceous perennial having a ligneous base. As the author's description has distinguished it from the other Mexican species, chiefly by the leaves and phyllaries, it is clear that all four species are similar in their shrubby or near shrubby nature. It was possible to include the American species in this study.

Garberia

Another shrub of this subtribe is found in the genus *Garberia*. When cataloguing a collection of plants that had come from east Florida, Nuttall (Amer. Jour. Sci. 5: 299, 1822) gave a brief Latin description of *Liatris fruticosa*. It was the only species of that genus referred to as fruticose by DeCandolle (Prod. 5: 132, 1836) and became the subdivision *Suffruticosae* in Torrey and Gray (Fl. N. Am. 2: 76, 1841). This plant, referred to by Nuttall in 1841 (Trans. Amer. Phil. Soc., ser. 3, 7: 285) as agreeing with the genus *Liatris* in its flowers but not in its habit, was transferred by Gray (Proc. Acad. Nat. Sci. 379, 1879) to the new genus *Garberia*. Thus it appears in more recent floras of the South as *Garberia fruticosa* (Nutt.) Gray. The restudy of William Bartram's plants (Bartr. Trav. 164, 1791; ed. 2 162, 1792) by Merrill (Bartonia 23: 24, 1944) called for a new combination. After Dr. Francis Harper had covered Bartram's routes, he was satified that what Bartram had described as *Cacalia heterophylla* was the same shrub. The plant is now known as *Garberia heterophylla* (Bartr.) Merrill & F. Harper. It still is the only representative of the genus.

Carphephorus

The genus *Carphephorus* was established by Cassini (Bull. Soc. Philom. Paris p. 198. Dec., 1816) when naming as *C. pseudo-liatris*, a specimen without locality, seen in the Jussieu herbarium, which for a time was thought to be of Siberian origin. In his Dictionnaire, Cassini (Dict. Nat. Sci. 7: 148, 1817) explained that it belonged to the natural Tribe *Eupatoricae*, "section des *Liatridees*," in which he was placing it, near *Liatris*, the chaffy receptacle being the chief point of difference. Cassini's "sec-

tional" name must be rejected because under the international code a section is of infra generic rank, while Cassini applied this term to a group of genera. Torrey and Gray (1841) found that the character of the receptacle had been overlooked by some in describing other species and rightly recognized *Carphephorus* as an American genus. At that time, three other species were transferred from the genus *Liatris*, *L. bellidifolia* and *L. tomentosa* (Michx. Fl. Bor. 20: 93, 1903) and *L. corymbosa* (Nutt. Gen. 2: 132, 1818). At the same time also the older synonyms were given for these four species, as they were given by Gray (Syn. Fl. 1(2): 1886); hence they have not been repeated here. They still remain the four accepted species of the genus and all have been represented in this study.

Two Californian plants described as *Carphephorus junceus* Benth. (Bot. Sulph. 21, 1844) and *C. atriplicifolia* Gray (Proc. Am. Acad. Arts & Sci. 5: 1591, 1861) were early placed in the *Helanthoideae* instead of the *Eupatorieae*, and assigned to a new genus *Bebbia* by Greene (Bull. Cal. Acad. Sci. 1: 179, 1885). Thus though appearing under the genus *Carphephorus* on page 113 in Gray (Syn. Fl. 1(2) 1886), they are given under *Bebbia* in the supplement of that volume (p. 453). More recently, *B. atriplicifolia* (Gray) Greene has been reduced to varietal rank by I. M. Johnston (Proc. Cal. Acad. Sci., ser. 4, 12: 1197, 1924) so that this genus includes one species, *B. juncea* (Benth.) Greene, its variety *atriplicifolia* (Gray) Johnston, and variety *aspera* Greene (l.c.), all removed from *Carphephorus*.

Other excluded names and species are:

Carphephorus baicalensis Adams in Mem. Soc. Nat. Moscou 5: 115 (1817); DC. Prod. 5: 132 (1836) — *Saussurea pycnocephala* Ledeb. according to Benth. & Hook., Gen. Pl. 2: 249 (1873).

Carphephorus cordifolius DC. Prod. 7: 267 (1838) = *Brickellia cordifolia* Robinson, Proc. Am. Acad. Arts & Sci. 47: 200 (1911).

Carphephorus revolutifolius DC. Prod. 5: 132 (1836) according to Benth. & Hook. Gen. Pl. 2: 249 (1873) "certainly from description, expelled from the genus."

Carphephorus triangularis (DC.) Gray Pl. Wright. 1: 86 (1852), ex Hemsl. Biol. Cent. Am. Bot. 2: 109 (1881); *Bulbostylis triangularis* DC. Prod. 7: 268 (1838) = *Eupatorium vitifolium* (Sch. Bip.) Robinson, Proc. Am. Acad. Arts & Sci. 51: 537–8 (1917), *Hebeclinium vitifolium* Sch. Bip. ex Klatt Leopoldina 20: 90 (1884).

Trilisa

For the genus *Trilisa*, which Cassini (Bull. Soc. Philom. Paris, p. 140, Sep., 1818) established two years after the genus *Carphephorus*, the type was *Liatris odoratissima* Willd. (Sp. Pl. 3: 1637, 1803). Willdenow had taken up this name from Walter's *Anonymos odoratissimus* Walt. (Flor. Carol. 198, 1788), as he had also *A. paniculatus*, these names being declared illegitimate by article 33 of the International Code of Botanical Nomenclature. In his key of the *Eupatorieae*, Cassini (Dict. Sci. Nat. 26: 228, 234, 1823) placed this new genus in his section "*Liatridees*" between *Carphephorus* and *Suprago*, a name which has been retained for the plu-

mose section of *Liatris*. However, Cassini's genus was not accepted at once. DeCandolle (Prod. 5: 131, 1836) used it as a sectional name of the genus *Liatris*, and this was followed by Torrey and Gray (Fl. N. Am. 2: 76, 1841). The latter, however, correctly eliminated unrelated species and limited it to these two, collecting their older flora- and plate-references not included here. Since Bentham and Hooker (Gen. Pl. 2: 248, 1873) referred to the incorrect use of Cassini's generic name for a section, there has been no further confusion of this small genus.

One further species has been added. Small (Bull. Torr. Bot. Club 51: 392, 1924) had described a new plant from Florida under a generic name, an anagram of *Trilisa* which it resembled somewhat in habit, as *Litrisa carnosa*. When Robinson (Contrib. Gray Herb. new ser., 6: 104, p. 49, 1934) closely compared the plant with *Trilisa* and *Carphephorus*, he was led to refer it to the former genus.

MATERIALS AND METHODS

The same methods have been employed as were used in the study of *Brickellia* (Gaiser, l.c.). As some of these materials were collected along with those of *Brickellia*, frequently preparations of both were carried along together so that there might be as little variation in treatment as possible. Whenever seeds were received on herbarium specimens or in packets from other collectors,[2] they were germinated and eventually treated by the same variety of techniques and stains. In the preparation of figures of the chromosomes, the same photographic and microscopic equipment has been used at the same magnification, with the intention of making adequate comparisons of the size and morphology of the chromosomes with those of *Brickellia*. Thus not only the same terms are used, but with the same connotation of size. The same precautions were taken to study a sufficient number of cells so as to be able to choose similar stages for comparison of the chromosomes of all species of the different genera. Usually comparable stages of each have been photographed, but where the illustrations represent slight variations of condensation, the purpose of the selection has been discussed. In this study, use has been made of the photographic lens to illustrate the trichomes and epidermal figures, both to elucidate and confirm the drawings used for *Brickellia*.

In Table I are given the list of accessions of each species received along with the place and date of collection and the collector's name and number.[3] They have been arranged and discussed in the order of a key prepared for the genera (see page 124). As it has been impossible so far to obtain seeds or any cytological material of even a single species of *Kanimia* from South America, that genus is not included in this key.

Following the pattern of the investigation made of *Brickellia*, leaves of the species of these genera were similarly cleared for the study of trichomes.

[2] The author again expresses deep gratitude to all contributors.

[3] Reference to the numbers of collectors will permit examination of a number of specimens in various herbaria. Specimens collected or received by the author will be deposited in the Gray Herbarium.

As stated there, presence or absence of trichomes was not considered important for these studies. Attention was given to their form, as that has been found to change little, if at all, under varying environmental conditions. The terms applied in the descriptions and figures 61 to 88 of *Brickellia*, have again been used here. The same principle was adopted of obtaining leaves at the Gray Herbarium of specimens which had been referred to by authors so that they would approach the typical. As these genera are comparatively small, it was possible to examine one to several leaves of almost all the species and their varieties. It must be pointed out that it does not represent an examination of leaves of numbers of specimens of any species. The difference in upper- and lower-most cauline leaves were illustrated for one species, *Trilisa paniculata*. Changes in the ontogeny of the species were not generally studied in detail.

OBSERVATIONS

I. Seedling growth

Whenever possible, an effort was made to grow some of the germinating seeds for a time at least, in the greenhouse. Attempts to bring the plants into bloom met with varying success. Of three species of *Carphephorus*, two of *Trilisa* and the one *Garberia* none ever produced flowering axes under the same conditions which stimulated flowering of more than a dozen species of *Brickellia*, three species of *Kuhnia*, two of *Barroetea* and one of *Carphochaete*. At least several plants of *Trilisa paniculata* were kept for more than three years, a period longer than normally would be required for a biennial plant to come into flower, and above ground they still had only rosettes of leaves. Time and facilities did not permit further studies along this line.

The plantings attracted attention because of the striking differences of the seedling conditions. As has been described and illustrated for eighteen species of *Liatris* (Gaiser 1950a), during the first season, while the primary root is becoming very much thickened, those seedlings produce only radical leaves. As can be seen in figures 42 to 62, the larger ones with a longer growing period, have formed quite a rosette. Then in the second season, usually a flowering spike is produced. This was also illustrated in the progeny of a natural hybrid (Plate II c, Gaiser 1951). Young plants of *Liatris punctata* were here compared with those of the other genera.

In figures B and C are shown seedlings of *Carphephorus pseudo-liatris* II and *Trilisa paniculata* VIII, of approximately sixteen and eighteen months respectively, in comparison with one of *Liatris punctata* (Fig. A) of approximately two years. The latter is old enough to show the beginning of a forking and the subsequent elongation into the deeply penetrating system which is characteristic of this species. In the *Trilisa*, the modification to the thickened somewhat tuberous roots is already evident and to a lesser extent in the younger *Carphephorus* also. At maturity, a similar thickened fibrous condition would develop, for that is common to all the species of the genus. This photograph happens to illustrate the aptness

TABLE I

Chromosome Numbers in the *Kuhniinae*

Name	Growth Form	Accession No.	County	Locality of Collection	Collector, No. & Date	Chromosome Number n	2n
Carphochaete Bigelovii	Shrub	II	Pima Co., Ariz.	Santa Catalina Mts.	K. F. Parker 7274, 4/29/50		22
Garberia heterophylla	Shrub	IV	Volusia Co., Fla.	North of Ormond	Mrs. H. Butts, Dec., 1947		20
		V	Highlands Co., Fla.	e. of Sebring, Arbuckle Creek	R. Garrett 11/21/48		20
		VI	Flagler Co., Fla.	Korona	R. B. Miller, 2/16/50		20
		VII	Marion Co., Fla.	Ocala Natl. Forest, near Eureka	Miss L. E. Arnold 2/2/50		20
		VIII	Putnam Co., Fla.	10 mis. s.e. of Interlachen	W. B. Fox, 11/18/51		20
Carphephorus pseudo-liatris	Perennial herb	I	Liberty Co., Fla.	3 mis. e. of Hosford on Hwy. #20	H. Kurz, 11/5/49		20
		II	St. Tammany Parish, La.	1 mi. from Slidell on LaCombe Rd.	L. Ewan 19236, 11/25/49		20
C. bellidifolius	Perennial herb	II	Wake Co., N. C.	2 mis. s. of Fuquay Springs on U.S. #15 A	R. K. Godfrey & W. B. Fox 48679, 10/16/48		20

C. tomentosus	Perennial herb	I	Pender Co., N. C.	10 mis. s. of Harrel's store	R. K. Godfrey 12/22/51		20
C. corymbosus	Perennial herb	I	Alachua Co., Fla.	Gainesville	Miss L. E. Arnold 11/19/46		20
		V	Putnam Co., Fla.	10 mis. s.e. of Interlachen	W. B. Fox, 11/18/51		20
Trilisa paniculata	Perennial herb	II	Volusia Co., Fla.	n. of Ormond	Mrs. H. Butts Dec., 1947		20
		VIII	Leon Co., Fla.	23 mis. w. of Tallahassee	H. Kurz 11/5/49		20
		IX	Leon Co., Fla.	23 mis. w. of Tallahassee	H. Kurz 11/5/49		20
T. odoratissima	Perennial herb	I	Alachua Co., Fla.	Gainesville	Miss L. E. Arnold 11/19/46		20
		IV	Highlands Co., Fla.	Along Jackson Creek, near Sebring	R. Garrett 11/10/48		20
		V	Leon Co., Fla.	23 mis. w. of Tallahassee	H. Kurz 11/5/49		20
		VI	St. Tammany Parish, La.	1 mi. w. of Slidell	L. Ewan 19237 11/25/49		20
T. carnosa	Perennial herb	III	Highlands Co., Fla.	w. of Sebring	R. Garrett 11/11/48		20
		IV	Highlands Co., Fla.	wet pinelands s. of Sebring	R. Garrett 11/4/49		20

TABLE I — *continued*
Chromosome Numbers in the *Kuhniinae*

Name	Growth Form	Accession No.	County	Locality of Collection	Collector, No. & Date	Chromosome Number n	2n
Kuhnia eupatorioides var. *pyramidalis*	Perennial herb	I	Kalamazoo Co., Mich.	Sect. 29, Schoolcraft Twsp.	C. R. Hanes 9/17/47		18
		II	Clark Co., Ky.	12 mis. e. of Winchester	F. T. McFarland 10/18/47		18
		III	Brazos Co., Texas	5 mis. s. of College Station	H. B. Parks 10/20/47		18
		VII	Kalamazoo Co., Mich.	Along L.S.M.S. Rwy., Schoolcraft Twsp.	C. R. Hanes 1648 10/5/48		18
K. eupatorioides var. *texana*	Perennial herb	I	Dallas Co., Texas	3100 Block on Rosedale St., University Park, Dallas	L. H. Shinners 11/11/48	9	18
K. eupatorioides var. *corymbulosa*	Perennial herb	I	Roosevelt Co., Mont.	10 mis. n.e. of Poplar	M. Ownbey 3229 8/30/49		18
K. Mosieri	Perennial herb	I	Alachua Co., Fla.	Gainesville	R. Garrett 11/3/48	9	18
K. rosmarinifolia	Perennial herb	III	Santa Cruz Co., Ariz.	Shaded canyon, Patagonia	D. H. Darrow & Haskell 2317 10/14/44	9	18
		V	Apache Co., Ariz.	Near cultivated land, St. John's	K. F. Parker 7409 12/3/50		18

K. Schaffneri	Perennial herb	I	Mexico, Mex.	Hills of El Salto, n.w. of Huchuetoca	D. B. Gold & F. Matuda 10/30/51		18
Barroetea subuligera var. *latisquama*	Perennial herb	I	Jalisco, Mex.	Along rocky cut near top of barranca, Guadalajara	L. O. Gaiser 66 10/27/50	9	18
B. sessilifolia	Annual	I	Puebla, Mex.	Along dry slopes of Cerro Tlacoctli 6 kms. s. of Izucar de Matamoros	L. O. Gaiser 75 10/31/50	9	18
		II	Morelos, Mex.	From the limestone mt. at Yautepec	L. O. Gaiser 76 11/3/50		18
		III	Morelos, Mex.	ca. 23 kms. from Cuernavaca on mt. slopes on road to Yautepec	L. O. Gaiser 77 11/3/50	9	18
		IV	Guerrero, Mex.	5 kms. from Taxco, along Mexico to Taxco Hwy.	L. O. Gaiser 88 11/4/50		18

Chromosome Numbers in the Subtribe *Ageratinae*

Mikania scandens	Vine	II	Calvert Co., Maryland	Plum Point	S. F. Blake Autumn 1946		38
		III	Flagler Co., Fla.	Haw Creek Region	Mrs. H. Butts Autumn, 1946		38
		VII	Highlands Co., Fla.	Rich wet soil, Sebring	R. Garrett 11/15/48		38
M. cordifolia	Vine	I	Highlands Co., Fla.	Highlands Hammock, State Park	R. Garrett 11/23/48		38

SEEDLINGS

of the specific name *pseudo-liatris*, given by Cassini to his type species of the genus. While narrower, linear leaves are found in a number of species of *Liatris* other than *L. punctata*, this is the only species of *Carphephorus* possessing them. It is obvious that regardless of the shape and the structure of the root, development of a rosette of leaves is common to all and is of rather prolonged duration. At least under greenhouse conditions, this same *Trilisa* seedling has not varied much in appearance in more than three years.

Figures D to G represent comparatively much younger seedlings of *Carphochaete Bigelovii* II, *Barroetea sessilifolia* I, *Kuhnia rosmarinifolia* V and *Brickellia adenocarpa* III. Only records were kept of the time of sowing the seeds, so that from those dates, the *Carphochaete* is a little more than a month old, the *Barroetea* is less than three months, the *Kuhnia* a little more than two months and the *Brickellia* less than two months. All have developed slender fibrous roots at this time but already show a fast growing stem-axis with a number of nodes and internodes. This similarity in seedlings cannot be attributed to any likenesses of their actual growth-form, for while this species of *Barroetea* is an annual and might be expected to show very rapid growth, that of the *Kuhnia* is an herbaceous perennial, that of the *Brickellia* a shrubby perennial, and the *Carphochaete* a small shrub.

The matter of chief interest was that there were two types into which all of these seedlings can be classified: the rosette and the non-rosette.

II. Chromosome Number and Morphology

Carphochaete

Cells of *Carphochaete Bigelovii* II were found to have a noticeably greater amount of chromatin than any of the other genera studied. This is due first of all to a larger number of chromosomes ($2n = 22$) but also to the presence among them of a majority of larger ones. While the exact size and form of all the chromosomes is not evident in figure 30, among the thirteen peripherally arranged units can be distinguished some of the long and medium classes.[4] The V approximately at the center top and the one almost at the center bottom, are designated medium in length (Mm), in contrast to the two long V's along the right (Lm), all of these being medianly constricted. The latter two in turn are distinguished from

[4] The same abbreviations as have been used in Gaiser (1953) are here applied: Using capital letters to express length, long chromosomes with median, submedian and subterminal constrictions are represented as Lm, Lsm, and Lst respectively, chromosomes of median length similarly constricted as Mm, Msm and Mst, and short chromosomes similarly Sm, Ssm and Sst. The short short class became SS; when medianly contricted SSm and when terminally SSt.

Explanation of Figures of Seedlings

Figures represent seedlings of various accessions of different dates. Figs. A–C photographed 5/9/51. Figs. D–G photographed 4/26/51.

A. *Liatris punctata* 11/22/49. B. *Carphephorus pseudo-liatris* II 1/19/50. C. *Trilisa paniculata* VIII 11/22/49. D. *Carphochaete Bigelovii* II 3/20/51. E. *Barroetea sessilifolia* I 2/26/51. F. *Kuhnia rosmarinifolia* V 2/15/51. G. *Brickellia adenocarpa* III 3/5/51.

two of similar length but having submedian constriction (Lsm), at right and left at the top, and a pair along the left side, in slightly lower focus, which are subterminally constricted (Lst). With the remaining marginal V at the lower left clearly a long chromosome also (Lm), a total of seven of the long class have been counted merely among the peripheral ones. As frequently occurred, toward the center among others, are six shorter units (Sm) of which two can be distingiushed at lower left. In a similar cell (Fig. 29) of a Feulgen preparation, only one medium chromosome was left with these six, all of which are short V's and medianly constricted, to fill the center around which fifteen long and medium ones were arranged marginally. There is a sharper break between the six short ones and the remaining sixteen than separates the equal number of long and medium ones into which that number has been divided. In the short ones there was little doubt that the constriction was median. The eight long chromosomes were analyzed as to centromere position with less difficulty, than those of medium length where there was some uncertainty. From the study of material available of one accession the karyotype has been given in Table II as: 2 Lm, 4 Lsm, 2 Lst, 4 Mm, 2 Msm, 2 Mst and 6 Sm.

GARBERIA HETEROPHYLLA

This monotypic species, restricted to Florida, was received through five different collectors from as many different counties. Excellent material was available for study and no variation was found. In a cell (Fig. 28) of accession VI from Flagler County, the number of chromosomes can be counted (2n = 20) and their morphology is also clearly recognizable. Thus, by beginning as at twelve, and proceeding clockwise around the dial, the marginal chromosomes represented in succession are as follows: Mst, Lst, Sst, Lsm, Mm, Msm, Lm, Lsm, and Sm. In the cell there are a pair of each of these classes except Mm, and of that there are three pairs. A second cell (Fig. 27) in the same section, shows that two of the shortest units, lower left and right margins, are heterobrachial. This was more convincing in cells particularly favorable for study of accession VII, though not photographed to much better advantage (Fig. 26, 3rd from left at top). By comparison with the cells of *Carphochacte* there is this difference of the fewer (four rather than six) chromosomes of the short class, and in their variation from the uniformly similar isobrachial type. As for the rest, the same classes are present though not to the same numbers. With one pair of long of each of the three constriction types, rather than a total of eight long ones, comes a further reduction in amount of chromatin. This karyotype has the greatest variety: 2 Lm, 2 Lsm, 2 Lst, 6 Mm, 2 Msm, 2 Mst, 2 SM, and 2 Sst.

CARPHEPHORUS

Two of the four species of *Carphephorus* were examined from at least two accessions, while *C. tomentosus* and *C. bellidifolius* were limited to one each. In all, the 2n chromosome number was found to be 20.

Of *C. bellidifolius* there were a number of excellent cells for study.

From comparisons made with *Carphochaete Bigelovii* it was observed that the chromosomes were all more nearly equal in length. Two pairs of medium chromosomes one each with medium, Mm, and submedian, Msm, constrictions, were almost as long as the long chromosomes. Also the next to the shortest pair were not sharply different from the medium in length. Frequently when the karyotype was assembled after an analysis of a cell, there were odd numbers for these two classes. The slightly more condensed chromosomes of figure 22 were well spread. Beginning as at seven and proceeding clockwise to four, the marginal ones are: Mst, Mm, Mm, Lst (pale, as slightly below focus), Lsm, Mm, Mm, Mst, Lst, Lm, Msm, and Msm. The two latter and the pair, Mm, directly opposite, closely approach the long ones. In this cell the shortest units are toward the center.

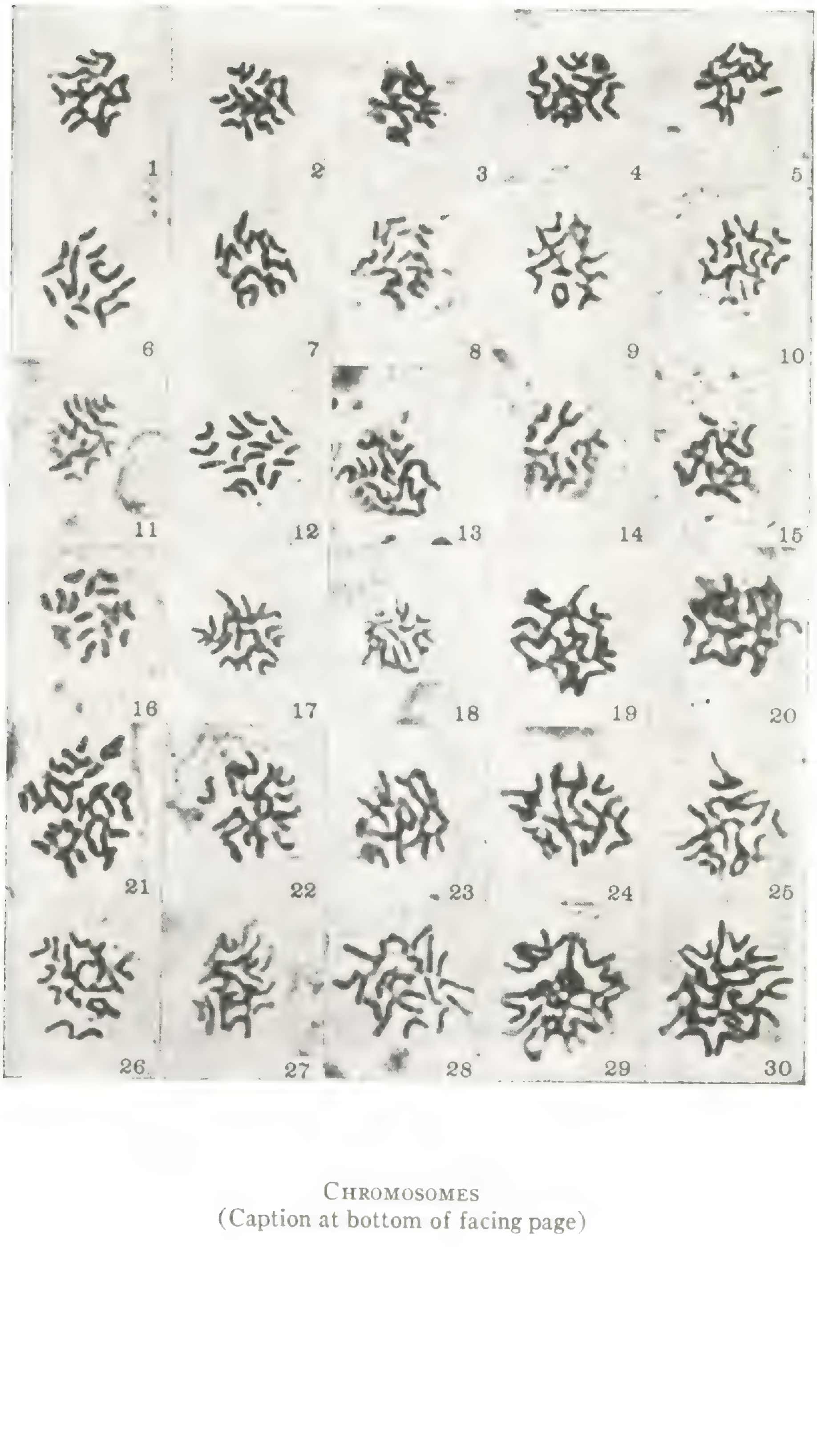
Preparations from seeds of *Carphephorus tomentosus*, which had been received from North Carolina, were more adequate for study than photography. As in the cell of figure 23, the chromosomes may be spatially separated but slight overlapping of the ends confuses the picture. Under the studies of this species the note had been made "remarkably few short chromosomes."

As was customary accompanying the studies of cells, diagrams of *C. corymbosus* V were made and the pairs of chromosomes numbered in succession as to their lengths. With a total of twenty chromosomes, the numbers of the shortest pairs were 9 and 10. While the latter was sure to be of the class Sm, opposite 9 there was frequently placed the question, "short or medium." In figure 24 for example, along the right side two isobrachial chromosomes which are clearly medium in length, alternate with two which are heterobrachial. These latter were numbered 9 and 8 respectively, meaning that while the bottom one was one of the characteristic medium pair with subterminal constriction, Mst, the second from the top was of the questionable class.

Accessions of *C. pseudo-liatris* from Florida and Louisiana were compared. Because tips were available from seedlings (see Fig. B) growing in a pot, as well as from germinating seeds, the most convincing analysis of the morphology of the chromosomes was made of this species. In figure 25, photographed when one each of the two shortest pairs are in focus, a number of the longer chromosomes are foreshortened. Almost at center bottom is a short medianly constricted chromosome, Sm, while the second from the center top is heterobrachial. Frequent analyses left a question concerning the members of this pair, just as had been the case in studies of the other species. Certainly no marked difference was noted for any one. Therefore one karyotype has been given for the four of them: 2 Lm, 2 Lsm, 2 Lst, 6 Mm, 2 Msm, 4 Mst, and 2 Sm. This modification of the two last classes was made with hesitation but allowing for the factor of human error, was accepted on the evidence of the camera.

Trilisa

Of several collections of *Trilisa paniculata*, made in South Carolina in October, germination of seeds was very poor, though it was possible to



CHROMOSOMES
(Caption at bottom of facing page)

obtain the chromosome count, 2n = 20. More somatic divisions were obtained from two accessions from northern Florida in November and a few seedlings were grown (see Fig. C). While a majority of longer chromosomes in a peripheral arrangement was the more usual, in figure 19 some of the medium and short units are seen in this position. Thus a better idea of the comparative lengths of all the classes of units for this species is obtained. At the top left corner, two medium chromosomes, the one subterminally, Mst, and the other medianly, Mm, constricted, lie respectively below and above a long submedian one. The mate for the former appears at the opposite right hand corner between two radiating long chromosomes of subterminal constriction, Lst. Below these, one each of the longest and shortest medianly constricted chromosomes are sharply contrasted and followed by a similar one medium in length. The latter is one of the medium class which approaches the long. Certainly this medium chromosome and the long one are more nearly equal than it and the short one. In size and form no noticeable variation from the chromosomes of the species of *Carphephorus* was evident. Comparison of this cell with figure 24 of *C. corymbosus* brings the camera's confirmation. The same question arose as to the length of the pair next to the shortest, but they were considered to be heterobrachial and not unlike the class Mst.

Preparations were made from seeds of *Trilisa odoratissima*, known as the Vanilla Plant, from Florida and Louisiana. The long chromosomes were more prevalent and of the same form as in the previous species. Also, there was no evidence that the medium and short ones differed. Because of the abundance of cytoplasmic inclusions in the cells of this species, fewer cells were suitable for photography. When the chromosomes were well spread, globules were often overlying. It would have been better to have made all preparations by the Feulgen technique. Figure 20 is of a cell just back of the meristematic apex and the chromosomes are therefore more crowded. One karyotype is believed to be common to these two species and it has been found to be indistinguishable from that of *Carphephorus*.

EXPLANATION OF FIGURES

Figs. 1–7, 9–30, are from near comparable metaphase plates in root-tips. Fig. 8 is of an early anaphase plate. 1, 2, 3. *Barroetea sessilifolia* I. 4, 5. *B. subuligera* var. *latisquama* I. 6–10. *Kuhnia eupatorioides* var. *pyramidalis*; 6–8. (III from Texas), 9. (II from Kentucky), 10. (VII from Michigan). 11. *K. eupatorioides* var. *texana* I. 12. *K. eupatorioides* var. *corymbulosa* I. 13. *K. Mosieri* I. 14–16. *K. rosmarinifolia*; 14, 15. (of accession III), 16. of V. 17, 18. *K. Schaffneri* I. 19. *Trilisa paniculata* VIII. 20. *T. odoratissima* IV. 21. *Mikania scandens* III. 22. *Carphephorus bellidifolius* II. 23. *C. tomentosus* I. 24. *C. corymbosus* V. 25. *C. pseudo-liatris* I. 26–28. *Garberia heterophylla*; 26. of accession VII, 27, 28. of VI. 29–30. *Carphochaete Bigelovii* II.

Preparations made of root-tips taken from plants, fixed in Belling's at the same time and stained in toto in Feulgen's, Figs. 5, 11, 12, 25, 29. Root-tips of seeds after Belling's and stained in N.G.V., Figs. 16, 24; after Karpechenko's and stained in Feulgen's, Figs. 9, 18, 27, 28. All the rest were of seeds fixed in Karpechenko's and stained in N.G.V. The photomicrographs were taken with the use of a Zeiss microscope and a Homal IV lens. All figures 2300x. Reduced 1650x in reproduction.

The preparation of the plates has been aided by a grant from The Society of Sigma Xi, which the author gratefully acknowledges. It is a pleasure to acknowledge the assistance of Mr. Paul Brown in the photomicrography.

The rarer species, *Trilisa carnosa*, limited to Florida, which had been thought to merit new generic rank by Small, was received from the same locality near Sebring, three times from October to November, 1948, and again in November, 1949. The difficulty of germinating seeds of this species was certainly not overcome during the time and with the material available. Only a few seeds ever appeared to begin growth and none developed very far so that an extremely limited number of mitoses were found. The number ($2n = 20$) and approximately the same kinds of chromosomes as found in the other two species were sketched from cells not adequate for photography. However, lacking sufficient material for careful studies, the karyotype of this species cannot be included at this time.

KUHNIA

Three of the four American species given by Shinners (l.c.) have been available for this study. Accessions had been received of the largest, most widely distributed species, *K. cupatorioides* L. from the states of Michigan, Kentucky, Texas and Montana, which, according to Shinners (l.c.) would represent all the varieties of that species except *ozarkana* Shinners. Those from the first three sources were variety *pyramidalis* Raf. and from the last, var. *corymbulosa* T. & G. while Dr. Shinners himself contributed a packet of seeds of his variety *texana*. A glance at figures 6 to 12 of this polymorphic species, shows a chromosome plate of $2n = 18$, in which there are lacking any of the long chromosomes, so characteristic of the genera here previously discussed.

K. EUPATORIOIDES variety PYRAMIDALIS. From preparations of particular clarity, stained with Newton Gentian Violet five years ago, the sizes of the chromosomes can be shown. At the lower left in figure 6, a parallel pair of the shortest and longest units, both medianly constricted can be compared with a single chromosome of intermediate length, lying almost horizontally above them. The units of this figure are probably all a little more condensed than those in figure 7, which is of a cell in a similar preparation. In the latter, the two longest chromosomes are at outer left and right and are submedianly constricted. From such figures, it is clear that the longest chromosomes would have to be placed in the medium class, according to the scale of sizes here used. One might then expect the shortest chromosomes, since there are units intermediate in length, to be two classes removed and to fall into a short short class, as adopted for some species of *Brickellia* (Gaiser 1953). Considerable effort was made to decide this question by comparison of various stages and of cells of all the accessions. Figure 8 is of an anaphase plate of a recent mitosis as can be judged by the parts of two chromosomes outlying in the cytoplasm at the right, belonging to the other closely overlying plate. The chromosomes are more slender but again they do not cover three distinct classes of length. It is considered that the karyotype includes medium to short chromosomes, and when there are nine pairs of such closely approximating lengths there is difficulty in deciding the boundary between the two classes.

In figure 8, two chromosomes with very small terminal bodies are seen, one at center bottom and the other at center left. More frequently cells were found in which only one such satellite was visible, as is shown at the end of the curved chromosome at upper right of figure 6 and at the inner end of the chromosome stretching toward the center from the left of figure 7. It is believed these chromosomes are next in length to the two longest pairs. By careful analysis of numerous cells of other accessions as well as this, next in succession of length are: 2 Msm and 2 Mm, which more closely approach the aforementioned three pairs than do the other 4 Mm. Whether the latter should be classed as short may be debatable. The four shortest are considered 2 Sm and 2 Sst. In preparations of accession II from Kentucky (Fig. 9) as well as accession VII from Michigan (Fig. 10) this analysis was also favored.

K. EUPATORIOIDES variety TEXANA. In the second accession from Texas, the figures are very much the same. Cells without any visible satellites were more frequently found than those showing them even delicately as in figure 11 (the second chromosome on the upper left) from a Feulgen preparation.

K. EUPATORIOIDES variety CORYMBULOSA. The western variety was received from Montana. Well spread chromosomes in the plate of such a cell as shown in figure 12 help to confirm the previous analyses. At the center on the left side is the medium chromosome with a satellite appearing knob-like at its inner tip and close to its centrally placed mate. Above them, occur one each of the longest of Msm and Mm respectively. The curved pair at center bottom are the second pair of so-called Msm while the two overlapping as a V at top are second in length of Mm. It is evident from such a preparation that no sharp line separates the classes of chromosomes. However, on the basis of comparison with those of the other genera the karyotype is believed to be: 8 Mm, 4 Msm, 2 M with sat., 2 Sm, 2 Sst.

Of the two other American species of *Kuhnia* included, the first is a restricted endemic in lower Florida. Two cells of *K. Mosieri* Small, in which the chromosomes were well separated by microscopic adjustment, could be seen in the field of the microscope at one time. Starting with the longest chromosomes, successively those next in size were sketched in different colors and the two cells constantly compared. Unfortunately they did not photograph as well as it was possible to draw them, to add to this interesting exercise. Of course there were points of indecision. However, even before it was recognized that in one of these (Fig. 13, center left) a chromosome with a satellite was represented, its arrangement in the order of consecutive chromosome lengths coincided with that given to such in *K. eupatorioides*. The karyotype of these two species were found indistinguishable. The second species is commonly known as *K. rosmarinifolia* Vent. Shinners (l.c.) considered this name a "nomen confusum" and put it in synonymy with *K. chlorolepis* Wooton & Standley. Blake (1942) did not consider it necessary to adopt this name in his treatment of the genus for Arizona and so I have not, as both accessions

TABLE II

Karyotypes in Species of Genera of *Kuhniinae*

Name	Accessions Studied	Chromosomes										Remarks
		Total Number	Number of pairs each									
			Lm	Lsm	Lst	Mm	Msm	Mst	M with sat.	Sm	Sst	
Carphochaete Bigelovii	II	22	1	2	1	2	1	1	....	3		
Garberia heterophylla	IV V VI VII	20	1	1	1	3	1	1	....	1	1	
Carphephorus pseudo-liatris	I II	20	1	1	1	3	1	2	....	1	....	1 Mst = S ?
C. bellidifolius	II	20	1	1	1	3	1	2	....	1		
C. tomentosus	I	20	1	1	1	3	1	2	....	1		
C. corymbosus	I V	20	1	1	1	3	1	2	....	1		
Trilisa paniculata	VIII	20	1	1	1	3	1	2	....	1	....	1 Mst = S ?
T. odoratissima	IV V	20	1	1	1	3	1	2	....	1		
Kuhnia eupatorioides var. *pyramidalis*	I II III VII	18				4	2		1	1	1	1 Msm and 1 Mm the longest, other Msm and another Mm next in length.
K. eupatorioides var. *texana*	I	18	....	....	....	4	2	....	1	1	1	
K. eupatorioides var. *corymbulosa*	I	18	....	....	....	4	2	....	1	1	1	
K. Mosieri	I	18	....	....	....	4	2	....	1	1	1	
K. rosmarinifolia	III V	18	....	....	....	4	2	....	1	1	1	
K. Schaffneri	I	18	....	....	....	4	2	....	1	1	1	
Barroetea subuligera var. *latisquama*	I	18	....	....	....	4	2	....	1	1	1	Ditto
B. sessilifolia	I III	18	....	....	....	4	2	....	1	1	1	

here studied came from that state. Of the preparations of *K. rosmarinifolia* III, the same repetition of statements could be made, cells showing a small satellite less frequently seen (Fig. 15, at the center top), than those without them (Fig. 14). Of accession V of this species, a plate of particularly condensed chromosomes was photographed (Fig. 16) to show the narrow gap between the shortest and longest units. Thus, for example, comparison with figures 25 (Gaiser 1953) of *Brickellia microphylla* where the chromosomes were shortened by paradichlorobenzene treatment, or figure 42 of *B. glomerata,* where a similar drastic shortening accidentally happened in one cell of a Feulgen preparation, emphasizes that there is a greater spread in the species of that genus where the karyotype includes long chromosomes.

One of the three species, which do not occur north of Mexico, *K. Schaffneri* Gray, was available for this study. Because the type sheet contains also a root of some legume, Shinners (l.c.) renamed the species *K. microphylla,* but Blake [5] considers this unjustifiable.

In a very clear early metaphase plate (Fig. 17) from a Newton Gentian Violet preparation, the range in size of the chromosomes is shown. One of the longest chromosomes, submedianly constricted (Msm) is at the upper right corner and two of the shortest ones, medianly constricted (Sm), can be distinguished as smaller V's among the central group, almost at center top and bottom. At this focus, one arm of several of the marginal V's has been foreshortened. Thus, for example, the chromosome at lower right is the other of the longest pair (Msm) and in succession the other two at center bottom represent medium chromosomes of the next category, Mm and Msm respectively. The straight medium chromosome, which is at a slight angle above the latter, is terminated toward the center by a small knob and is the equivalent of the chromosome with a satellite. The same can be seen in a cell of a Feulgen preparation (Fig. 18) at the tip of the chromosome coming into the small central upper space.

By comparison of figure 17 with that of *K. eupatorioides* var. *corymbulosa* (Fig. 12) of a cell similarly prepared, it might appear that the chromosomes of this species are generally longer, but this is merely so because it is a slightly earlier metaphase stage. It is worthy of note that in both of these cells there is a knob-like body at the end of a pair of the chromosomes. That its appearance cannot be attributed merely to this one kind of preparation is proved by the use of the same kind (e.g., Newton Gentian Violet) in illustrating *K. eupatorioides* var. *pyramidalis* (Figs. 6, 7, 8) and *K. rosmarinifolia* (Fig. 15) where it is seen separated from the chromosome. Yet the same is also visible in Feulgen preparations (see Figs. 11, 18). In summary, in any kind of preparation of all of the species of *Kuhnia* here studied, this very small terminal body, which has been called a satellite, may be found, whereas in similar preparations of the previous genera, no evidences of such has ever been seen. No variation from the

[5] *In litt.*

karyotype given for *K. eupatorioides* has been found in the three other species studied.

BARROETEA

The one perennial species which is somewhat woody at the base, *B. subuligera* (Schauer) Gray, is known from the northern boundary to Hidalgo, a central state in Mexico. The larger variety *latisquama* Greenman, was described from a specimen collected in Jalisco. A plant of this was collected in the barranca at Guadalajara and from seeds of it, a seedling was grown for a time in the greenhouse. From pollen mother cells as well as root-tips, the chromosome number was found to be the same as in the species of *Kuhnia* studied, n = 9 and 2n = 18.

A comparatively early metaphase of a root-tip cell shows the form of sixteen of the chromosomes, but two short ones which were lying one above the other, resulted in the oval body at the upper right of the figure (Fig. 4). One chromosome of greatest length, submedianly constricted, is seen at lower right and a second in length, medianly constricted, is plainly contrasted at center top with one of the shortest (Sm). By the scale of sizes used for the other genera, neither of the former would exceed the medium class. Thus the karyotype includes medium to short chromosomes only. In this cell a number of the heterobrachial chromosomes are found around the periphery and may appear to be more numerous than in a very comparable stage of a *Kuhnia*, e.g., *Kuhnia Schaffneri* (Fig. 17). However, their number is not greater and in other cells where the chromosomes are a little more condensed (Fig. 5) no confirmation is found of this difference. While no chromosome with a satellite is shown, its equivalent is probably represented in one of medium length, subterminally constricted, for the free terminal body was seen in some other cells.

Of the annual species, *B. sessilifolia* Greenman, seeds were collected from four different localities of three of the central states of Mexico and from root-tips of each, the chromosome number was found to be the same as that of the perennial species, 2n = 18. It was also possible to grow seedlings (see Fig. E) from two of these accessions and similar meiotic divisions were obtained, n = 9.

Figure 1 of *B. sessilifolia* III shows a metaphase stage comparable to that of figure 4 of *B. subuligera* and the sizes of the chromosomes are very similar. On one of the longest chromosomes, at upper left, a satellite is conspicuous. In cells of slightly more condensed chromosomes the same is visible (Figs. 2, 3, lower right). Examination of a number of cells of *B. sessilifolia* I resulted in the same analysis of medium to short chromosomes including one of the former showing a satellite, both in Feulgen and other preparations, either in cells of root-tips taken from the plant or from germinating seeds.

From this study of two species of *Barroetea*, it was found that they were more similar to, than different from, the species of *Kuhnia* seen. The points of likeness consist in having: the same number of chromosomes; chromosomes which range from medium to short across an indefinite

boundary, and, one pair of the medium chromosomes showing a satellite. Certainly no constant difference in the karyotype was detected. It is given as: 8 Mm, 4 Msm, 2 M with satellite, 2 Sm and 2 Sst.

SUMMARY ON CHROMOSOMES

As summarized in Table II.

1. *Carphochaete* is the only genus having 22 chromosomes.
2. All the species of the three genera, *Garberia*, *Carphephorus* and *Trilisa* have 20 chromosomes, in common with a majority of the species of *Liatris*.
3. Four of the seven species studied of *Kuhnia* and two of the species of *Barroetea* have 18 chromosomes, the same number that had been found in all of the examined species of *Brickellia*.
4. Monotypic *Garberia* and the one species studied of *Carphochaete*, are both distinct in their karyotypes. The latter has a greater proportion of long chromosomes with three pairs of isobrachial short chromosomes, while in the former, one of two short pairs are heterobrachial.
5. *Carphephorus* and *Trilisa* could not be distinguished by their karyotypes. Yet they varied from *Garberia* in a closer approach, if not equality, of the shortest heterobrachial pair to the medium class.
6. Long chromosomes are absent in the five species of *Kuhnia* studied, the karyotype consisting of medium to short ones. A pair of medium chromosomes have small satellites.
7. A similar closely graded series of short to medium chromosomes, of which one pair bears satellites, makes up the karyotype in the two species of *Barroetea* studied.

III. Trichomes.

As the type of *B. Pavonii* Gray is in the Boissier Herbarium, only six of the seven species of *Barroetea* could be included in this study of the trichomes of the leaves. Five were found to vary slightly in the abundance of non-glandular trichomes which are uniseriate (Metcalfe & Chalk 1950) and of the acuminate type according to the classification of *Brickellia* (Gaiser 1953). The size and the thickness of the wall of the trichome vary very little from species to species. Figure 31 represents that of the annual *B. sessilifolia* and fig. 32, generally a slightly larger form, that of *B. subuligera* var. *latisquama*, the perennial considered somewhat woody at the base. The sixth species *B. glutinosa* Brandegee, with leaves described as densely glandular-puberulent, was found to lack this type of trichome but to have the same biseriate glandular form described as being common to a number of species of *Brickellia*. Along the leaf margin these might be found from a few to seven or eight cells high (Fig. 33). If seen edgewise they appeared as a stipitate somewhat globular organ (Fig. 34). When the flat expanse of the leaf was examined, one saw their apices as two typical hemispherical cells (Fig. 35) or by focussing a little lower as rounded cells above the level of the leaf surface. Figure 36 was taken at

a still lower focus where the epidermal pattern, including a stoma, became evident, but the foreshortened trichome was merely a dark blur. Checking leaves of the other species for this type of trichome, it was found only very occasionally on the underside of the midrib near the petiolar attachment. However, the depressed gland, as used also for *Brickellia* (Gaiser, l.c.), and the punctate condition on the lower surface was common to all except *B. glutinosa* where it was lacking on the lower as well as the upper. As in *Brickellia*, this glandular trichome is a longer stalked condition of the short form arising from the epidermal layer in depressions below what is normally seen as the leaf surface. When a species characteristically develops the elevated form, none or very few, if any, are seen remaining sunken below the leaf surface.

No evidence was seen of the smaller uniseriate capitate glandular trichomes in any species of *Barroetea*.

All the species of *Kuhnia*, according to Shinners' classification, were represented and showed a little more variation in trichomes than those of *Barroetea*. On the upper surface of leaves of *K. adenolepis* they were the shortest, consisting of no more than two or three thick-walled cells, arising from a very heavily cutinized epidermis (Fig. 37). Those of *K. Mosieri* were comparatively short, but consisted of thin-walled cells, almost uniform in diameter, so that the trichome tapered very little (Fig. 38). On *K. Schaffneri* (Fig. 39) a more attenuate trichome, of approximately the same length but with heavier walls, showed a tendency towards the moniliform type of rounded bead-like cells. In all those having thick walls this character was prevalent as shown in the uneven-walled form of the scabroid leaf of *K. rosmarinifolia* (Fig. 40). All the succeeding longer ones have been figured at the same magnification (220 ×) just as all the shorter ones had, though they were more enlarged (530 ×). While those of *K. eupatorioides* var. *pyramidalis*, taken from our accession from Kentucky (Fig. 41) resembled that of *K. Mosieri* in the thinner and straight walls, those of varieties *texana*, *ozarkana* and *corymbulosa*, with successively thicker and rougher walls (Figs. 42–44) were attenuate and more moniliform. Those on the scabroid leaves of *K. leptophylla* var. *mexicana* (Fig. 45) and *K. orcithales* (Fig. 46) did not differ much from the latter. In these two species an occasional cell filled with an aggregate crystal was more commonly seen than in any other species. In all of them the apical cell is longer than the rest but would not be recognized as a cap cell, as in some species of *Brickellia*.

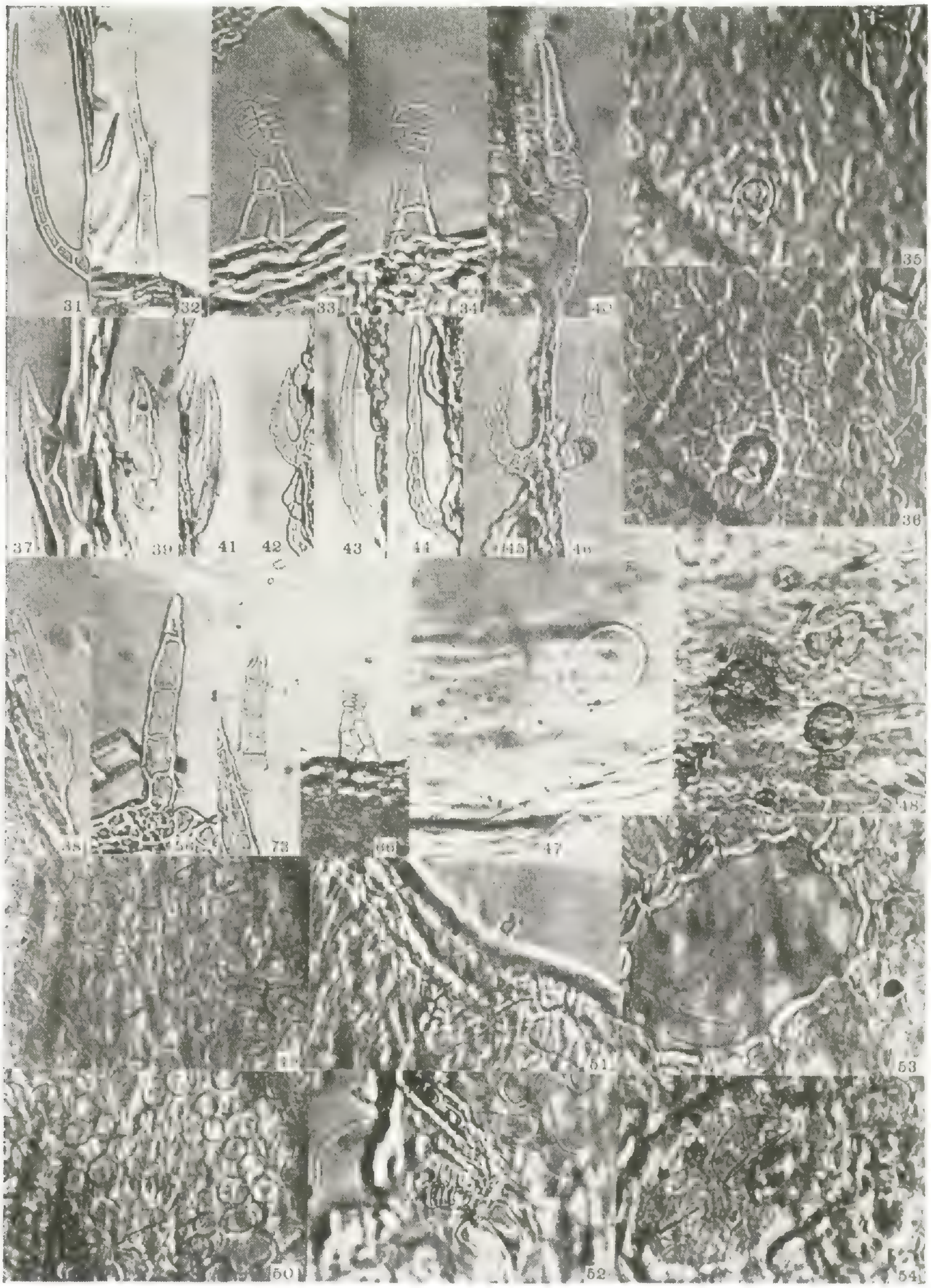
On no leaf preparation examined of any of the species of *Kuhnia* was evidence seen of the biseriate glandular trichome. By contrast the depressed gland and punctate condition was common to all species except *K. adenolepis*, and to both surfaces of the leaf, though generally it was less abundant on the upper.

What in *Brickellia* had been called uniseriate capitate glands, on stalks only a few cells in height, prevailed in all species. Generally they were small as in that genus, requiring a larger magnification for observation as well as photography as shown in Figure 47, 1100 ×, of *K. Mosieri*. An

exception to the general was found in *K. adenolepis*. This species had been distinguished by Robinson (1911b) because of its unique glandular ciliolate phyllaries, the glands being described as subsessile and black. The leaves had been described as "puncticulatis" on both surfaces. Very short trichomes have been described for the upper surface (Fig. 37). Examination of a cleared preparation of the type specimen revealed more abundantly on the lower surface, a gland that is a little larger than the previous (Fig. 48, 530 ×) and distinctive for its dark apical cell when the leaves of all species had been cleared similarly. It is possible that the apical or secretory cell in this species has a different content, as not only was it dark but as shown in the figure some of its secretion had plugged and darkened some of the sunken stomata, from which it had not completely dissolved. From the very evident secretory function of the apical cell of this uniseriate small type of trichome, which is so similar in form to that seen in *Brickellia* (Fig. 87, 88, Gaiser 1953), I have considered them glandular trichomes in these two genera as did also G. Fischer (according to Solereder 1908, original thesis not seen). Vuillemin (1884) had done likewise in *Cynara* and *Echinopus*, though there are no figures of those for comparison. They are quite unlike the bladder-like trichomes observed by Volkens (1887) in *Zollikoferia nudicaulis*, which are considered to be full of cell sap (Solereder 1908, Fig. 103E). In form, they resemble somewhat more the capitate hairs described by Rosenthaler and Stadler (1908, Fig. 28) for *Cnicus benedictus*, consisting of six to twelve cells, with an elongated terminal cell which were said to differ from the non-glandular hairs in having a richer content.

Two genera, *Garberia* and *Carphochaete* had been established as having entire leaves. Neither the single species of the first nor any of the four of the latter had trichomes comparable to those illustrated for the previous genera. They both had a more slender filamentous form somewhat prostrate over the surface of the leaf.

When Bartram first described *Garberia* under the name *Cacalia heterophylla* (see p. 90), he wrote of the fleshy leaves: "of a pale whitish green, both surfaces being covered with a heavy pubescence and vesicular, that when pressed feel clammy and emit an agreeable scent." It was no surprise then when both surfaces gave the familiar appearance of the punctate condition at a focus when stomata were clearly visible (Fig. 49) and of the paired hemispherical cells of the depressed gland (Fig. 50) by subsurface focusing. In addition, very narrow delicate filaments which tapered slightly if at all, and had cross walls at rather long intervals, lay twisted over the epidermis and proved difficult to follow to their origins. When the margin of this thick, entire leaf was examined it was possible by careful focusing to follow the epidermis as it alternately rose and fell into small pocket-like areas. In each depression was a tiered organ, two cells wide and approximately six cells high (Figs. 51, 52) familiar as the glandular trichome seen upon the leaf-surface of *Barroetea glutinosa* (cf. Fig. 33). In *Garberia* these arose in the epidermal layer from smaller cells which were clearly differentiated by their size. The first cells above

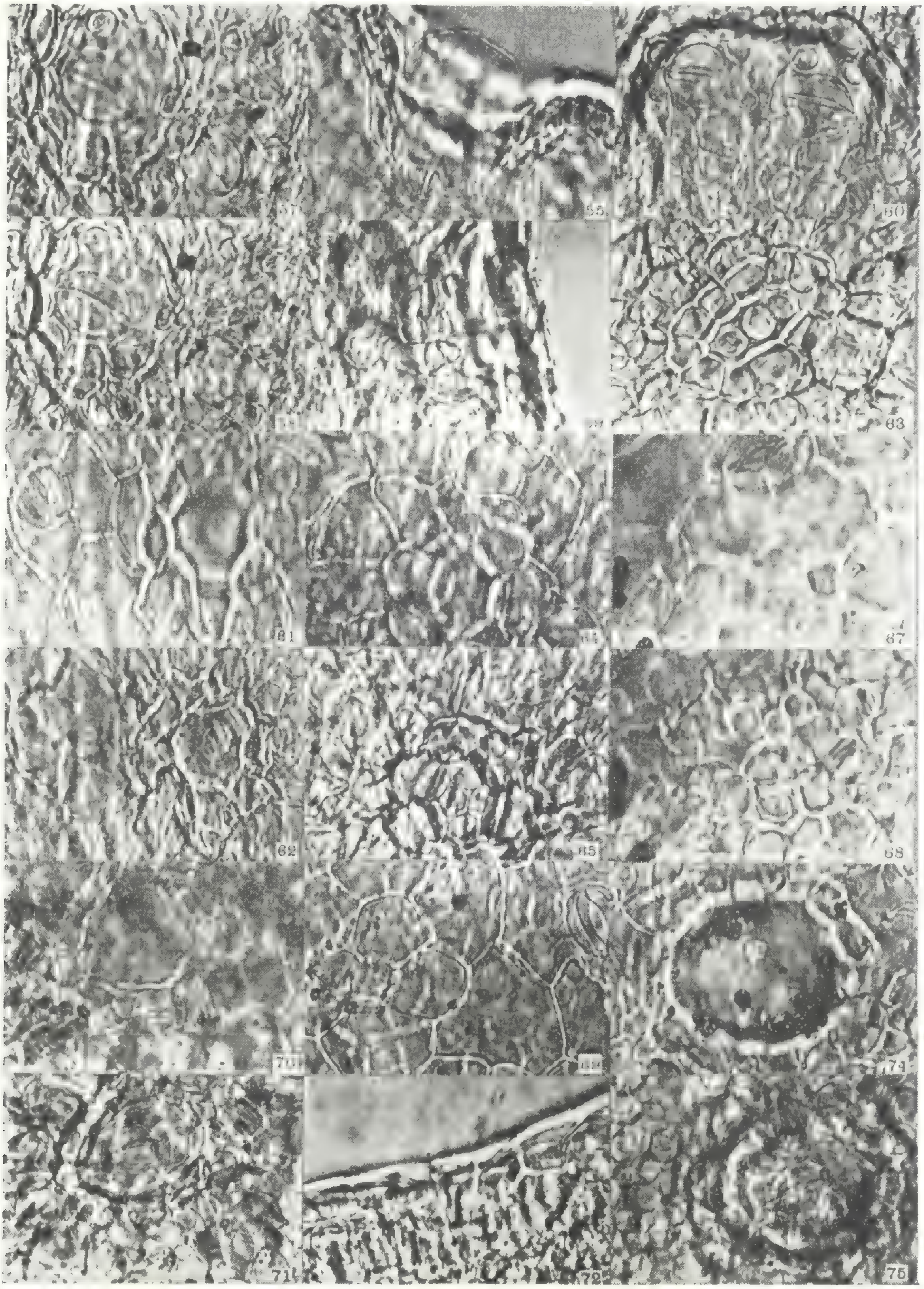


EXPLANATION OF FIGURES OF TRICHOMES

Figs. 31, 32, 37–46, 44–53, 56, 73. Non-glandular trichomes. Figs. 33–36, 66. Glandular biseriate trichomes. Figs. 47, 48. Non-glandular uniseriate trichomes.

31. *Barroetea sessilifolia*. 32. *B. subuligera* var. *latisquama*. 33–36. *B. glutinosa*. 33, 34. Along the leaf margin. 35. Above the epidermal surface. 36. At the epidermal surface. 37. *Kuhnia adenolepis*. 38. *K. Mosieri*. 39. *K. Schaffneri*. 40. *K. rosmarinifolia*. 41–44. *K. eupatorioides*. 41. of variety *pyramidalis*, 42. of var. *texana*, 43. of var. *ozarkana*, 44. of var. *corymbulosa*. 45. *K. leptophylla* var. *mexicana*. 46. *K. oreithales*. 47. *K. Mosieri*. 48. *K. adenolepis*. 56. *Carphephorus corymbosus*. 66. *Trilisa paniculata*. 73. *T. carnosa*.

All these photomicrographs were made from cleared leaves by use of a Zeiss microscope and a Homal IV lens, except Fig. 32, which is 110x. Figs. 38–46, 56, 66, 73, 85x. Figs. 31, 33–37, 48, 200x. Fig. 47, 430x.



EXPLANATION OF FIGURES OF DEPRESSED GLANDULAR TRICHOMES

Figs. 49, 53, 57, 61, 64, 67, 69, 70, 74, by focusing at the epidermal surface. Figs. 50, 54, 58, 60, 62, 63, 65, 68, 71, 75, by focusing below the epidermal surface. Figs. 51, 52, 55, 59, 72, lateral view seen along the margin of the epidermal surface of leaf.

49–52. *Garberia heterophylla*. 53–55. *Carphochaete Bigelovii*. 57–60. *Carphephorus tomentosus*. 63–65. *C. corymbosus*. 61, 62. *C. bellidifolius*. 67, 68. *Trilisa paniculata*. 69. *T. odoratissima*. 70–72. *T. carnosa*. 74, 75. *Liatris punctata*.

All these photomicrographs were made from cleared leaves by use of a Zeiss microscope and a Homal IV lens. x200.

these had thicker walls which generally reflected the light more than the thinner-walled upper cells. Alongside such a trichome frequently a slender filament could be traced until it pushed up to the leaf surface. In Figure 52 part of such a filament is recognizable after it emerged above the leaf, though it is seen less clearly along the right wall of the small depression. Closer microscopic observation of the surface of the leaf then made intelligible what had been baffling in several other genera as well. In addition to the paired hemispheric cells seen when focusing below the surface, an additional small round cell (shown at the bottom in figure 50) accounted for the delicate emerging filament seen on the surface. Thus they are really very delicate uniseriate trichomes of long, narrow, thin-walled cells growing from the sunken epidermal layer alongside the biseriate glandular trichomes.

Volkens (1890) described scattered groups of trichomes consisting of five or six which were uniseriate with whip-like tips, surrounding one central unstalked, biseriate, bladder-like gland (Pl. 8, Fig. 1) on the upper surface of the leaf of a plant labeled "*Baccharis Richardifolia*." A second species of the *Astereae*, *Olearia Hookeri*, was said to be very similar while on the other Compositae that he examined, the uniseriate elements were increasingly fewer. In two genera representing the *Eupatoricae*, *Eupatorium* and *Symphyopappus*, these trichomes might occur occasionally but lacked the characteristic thread at the tip. From his figure 4a, showing two hemispherical cells of *Symphyopappus*, it appears that the biseriate gland was depressed with only the uniseriate emerging above the surface. Thus while the latter (Fig. 4b) appears more torulate, the grouping might be similar to that described here for *Garberia*.

Carphochaete Bigelovii had been described by Gray (see p. 90) as puberulous and resinous punctate. On first examination of the leaf preparation with lower magnification, very numerous depressed areas were seen which were not all equal in size. Closer examination of one of the smaller, revealed besides the two large appressed hemispherical cells, several accompanying small round ones as the one seen in *Garberia*. The delicate filaments, of which the latter are the bases, were not as long and therefore did not appear as abundant over the surface. The larger areas might merely show central cells of a greater diameter but frequently they were the result of the confluence of two pairs (Fig. 54). In this figure there are in addition, the bases of three filaments, two of which are seen at the surface in figure 53. Since the leaves of this species are small but rigid it was possible again by focusing along the margin of a prepared leaf to obtain a lateral view of the gland (Fig. 55). Only the lowermost pair of cells were thick-walled in comparison with the several in *Garberia*. The walls of the cells immediately above were very thin and made it difficult to show that there was but one intermediate pair. It was clear that the uppermost secretory cells were very much expanded, thus contributing to their larger surface-appearance.

Although one of the four known species, *C. Wislizeni*, had been described as "not sprinkled with resinous dots," a leaf of a Pringle specimen

(#765) from the mountains near Chihuahua, where the type was collected, was found to be very similar to *C. Bigelovii*. All four species might differ slightly in the abundance but not in the form and the kind of contents in the depressions.

The species of *Carphephorus* may have the small, upper cauline leaves pubescent when the lower and radicle leaves are nearly glabrous. This is not a character peculiar to the genus. Solereder (1908) having generalized that in many genera only the youngest leaves, branches and leaf petioles are covered with glandular trichomes. Thus much would depend upon the choice of leaf for preparation. Of *Carphephorus*, in common with the other genera, lower larger leaves were examined, leaving to *Trilisa paniculata* the comparison of lower and upper ones.

In form, the non-glandular trichomes on the surfaces and along the margin of the basal leaves of each of the four species of this genus were of near uniform type, of broader cells than seen in species of *Kuhnia*. Though they varied in length and to a minor degree in thickness of wall, being thickest in *C. tomentosus*, the cylindrical shape of the component cells was remarkably constant. One of medium length of *C. corymbosus* is illustrated (Fig. 56).

It was in the punctate condition of the leaf that a greater difference was noted, as is reflected in the descriptions given by Torrey and Gray (1841): *C. tomentosus*, punctate; *C. pseudo-liatris*, sparsely punctate; *C. bellidifolius*, punctate with scattered impressed dots; *C. corymbosus*, sometimes obscurely punctate. From these phrases it was not clear whether the difference was merely one of abundance. Examination of these leaf preparations showed a considerable difference in glandular structures.

On either surface of a lower cauline leaf of *C. tomentosus*, the paired cells characteristic of the depressed gland were seen abundantly when focusing below the surface (Fig. 58) in contrast to the craters seen when stomata are in view (Fig. 57). As described in *Garberia heterophylla*, the two hemispherical cells were accompanied by small marginal circular cells which had been recognized as the median optical view of delicate filaments. Frequently two or three were found and since they appear in figure 57 they obviously reach the surface though none were found spreading over the epidermal cells. Looking along the margin of one of these lower nearly glabrous leaves which is entire, the lateral view of the biseriate trichome with accompanying filaments at the side was seen in the depressed areas (Fig. 59). To this species then, the term punctate, as understood for the previous genera, could certainly be applied. The depressions were conspicuous macroscopically and that may be facilitated by their greater size for it was found that often two glandular trichomes, each with several laterally placed filaments were within the margin of one depression (Fig. 60).

In the preparation of the other three species the surface pattern appeared quite different. In a similar leaf of *C. bellidifolius* there was no sign of the depressed gland of paired cells. Instead, one circular cell,

TABLE III

Types of Trichomes and Glands in the Epidermis of Leaves of Genera of *Kuhniinae*

Name	Elevated above the surface					Depressed (i.e., punctate)								Depressed (but not punctate)	
	Non-Glandular					Glandular									
	uniseriate, trichomes	uniseriate, capitate		Biseriate		Biseriate		Biseriate uniseriate		uniseriate		uniseriate in groups 1 to 4		secretory, uniseriate	
		upper	lower	upper	lower	upper	lower	upper	lower	upper	lower	upper	lower	upper	lower
Barroetea sessilifolia	acuminate				occasional on midrib		×								
B. subuligera var. *latisquama*	acuminate				Ditto		×								
B. laxiflora	acuminate				Ditto		×								
B. brevipes	acuminate				Ditto		×								
B. setosa	acuminate						×								
B. glutinosa	occasional			×	×		×								
Kuhnia eupatorioides var. *pyramidalis*	nearly uniform	×	×			×	×								
K. eupatorioides var. *texana*	attenuate towards moniliform	×	×			×	×								
K. eupatorioides var. *ozarkana*	ditto	×	×			×	×								
K. eupatorioides var. *corymbulosa*	scabroid moniliform	×	×			×	×								
K. rosmarinifolia	scabroid moniliform	×	×			×	×								
K. Mosieri	nearly uniform attenuate	×	×			×	×								
K. Schaffneri	slightly moniliform	×	×			×	×								
K. oreithales	scabroid moniliform	×	×			×	×								
K. leptophylla var. *mexicana*	scabroid moniliform	×	×			×	×								
K. adenolepis	very short	few	×												
Carphochaete Bigelovii								×	×						
C. Wislizeni								×	×						
C. Grahami								×	×						
C. Schaffneri								×	×						
Garberia heterophylla								×	×						
Carphephorus tomentosus	nearly uniform							×	×						
C. corymbosus	nearly uniform											×	×		
C. pseudo-liatris												×	×		
C. bellidifolius										×	×				
Trilisa paniculata				on upper cauline										×	×
T. odoratissima	nearly uniform													×	×
T. carnosa						×	×							occasional	

Types of trichomes as seen by microscopic examination of cleared leaves from annotated herbarium specimens at the Gray Herbarium. × indicates presence of.

larger than those accompanying the gland in *C. tomentosus*, appeared encircled by other leaf cells (Fig. 62). By focusing exactly on the surface, when stomata are visible, there was again a crater-like appearance in its place (Fig. 61). This gave confirmation that we were seeing the punctate equivalent for this species which had been characterized as "compressed dots," likely because they are smaller.

In *C. corymbosus* a similar arrangement of cells was characteristic but the center was usually composed of more cells. Figure 63 shows a frequent linear arrangement of three. When there were four such cells they conformed to the arrangement common to four spheres and the surrounding leaf cells had a circular form (Fig. 65). At the epidermal level with stomata visible, this also had the appearance characteristic of a punctate condition (Fig. 64).

In several preparations of *C. pseudo-liatris* the little evidence seen of glandular punctation indicated similarity to *C. corymbosus*.

Thus all four species are punctate, indicating the presence of a depressed gland or short glandular trichome. In *C. bellidifolius* there was a single or uniseriate condition while in *C. corymbosus* and *C. pseudo-liatris* there might be from one to a group of four of the uniseriate form. In *C. tomentosus* there was the familiar biseriate trichome accompanied by the uniseriate similar to *Garberia*.

From the time of Walter's original descriptions of the two species of *Anonymos* (see p. 91), *Trilisa paniculata* has been distinct from *T. odoratissima* in having a viscidly pubescent stem and upper cauline leaves. For this reason some of the latter as well as the lower glabrous leaves and in addition phyllaries of the inflorescence of this species were cleared. On both the phyllaries and small leaves, typical biseriate glandular trichomes were found (Fig. 66) very comparable to that figured for *Barroetea glutinosa*. Examination of either surface of a basal nearly glabrous leaf showed neither these glandular trichomes nor any trace of the typical depressed gland of two hemispherical cells. Instead rosette-like arrangements around a central cell were seen when viewed at a sub-surface focal level (Fig. 68). This figure does not appear unlike that of *Carphephorus bellidifolius* (see Fig. 62). However, when viewed at the surface the epidermal cells clearly adjoin the specialized cell (Fig. 67). This is confirmed in figure 69 of *T. odoratissima*, photographed at the surface and showing more clearly the secretory droplets. There is no indication of any marked depression in the epidermis of either species. This explains the inclusion of "not punctate with impressed dots" in the description of section *Trilisa* Cass. of *Liatris* by Torrey and Gray (l.c., p. 76) since they included only these two species at that time. At the surface the specialized cell hardly appears to be free from the surrounding cells of the epidermis. However, the fact that a central cell remains in focus from that layer through the next below, which shows distinct encircling cells, indicates that it is a secretory organ with a greater depth than one epidermal cell. None of these distinctive cells was found close to the thin margins of the leaves of these two species and so could not be studied laterally as was possible

in the preparations of *Garberia*, *Carphochaete* and *Carphephorus tomentosus*.

Trilisa odoratissima, commonly named the Vanilla Plant for the fragrance of the crushed leaves, has been used in the tobacco industry and is included in lists of drug plants. Therefore references [6] to the study of the structure of its leaves have been found in pharmaceutical journals.

Paschkis (1879) was probably the first to study the leaves microscopically. He described the upper and lower epidermis as including yellow spots, .015 mm. in size, which were surrounded by regular small epidermal cells. From tranverse sections he found these to be glands, in small clefts, consisting of a basal stalk cell wedged in between the two adjacent epidermal cells, and three to four additional ones. These rise just to the level of the other epidermal cells. He makes a point of their close envelopment by the thick cuticle of .008 mm., and as his figures show, the small depression in the epidermis is closely filled. This undoubtedly explains my failure to see any crater-like opening over the gland in surface view. The secretion, which is of such a pleasant odor when expressed, is due to cumarin. The diagram in Higley (1893) is very similar to the above description as is also the figure in Hanausek (1912) who called it a glandular trichome. From the relation to the leaf surface it has its origin as a depressed form. Among the multiple types found in these genera it is here termed uniseriate and not punctate.

In the leaves of the recently added third species, *T. carnosa*, the frequent appearance of a single central cell was again replaced by the two characteristic of the depressed biseriate gland (Fig. 71). By focusing on the surface when stomata are in view, the crater-like appearance of the punctate condition was again shown (Fig. 70). By carefully following around the margin of the leaf for any traces of the gland, only near the apex where it was thicker, a lateral view of one was seen (Fig. 72) giving evidence of at least an occasional uniseriate gland such as found in the previous genera. Certainly when examined microscopically the large basal leaf of *Trilisa carnosa* appears very different from those of its two congeners. However, in a similar way the biseriate glandular condition of one *Carphephorus* species, *C. tomentosus*, distinguished it from the other three.

No non-glandular trichomes were found on the lower leaves of the first two species and only an occasional short one near the petiole of *T. carnosa*. They were very similar to those of *Carphephorus* (Fig. 73).

Summary (re trichomes)

With the help of table III, the observations on trichomes and glands on basal cauline leaves can be summarized.

1. Non-glandular, uniseriate trichomes are lacking in *Garberia* and *Carphochaete* and show very little variation within three genera, being

[6] I am indebted to Prof. G. N. Hocking for these references.

acuminate in *Barroetea* and nearly uniform in *Carphephorus* and *Trilisa*. In *Kuhnia*, the largest of these genera, they may vary from being nearly filamentous or uniform to slightly tapering or attenuate. The thicker walled forms of the latter suggested the moniliform.

2. The elevated biseriate glandular trichome, comparable to that forming the indumentum in a number of species of *Brickellia*, was found only in one species of *Barroetea*.

3. The same structure sunken below the leaf surface, the depressed biseriate glandular trichome, was common to all the other species of *Barroetea* and to all species of *Kuhnia* and one of *Trilisa*.

4. In *Garberia* and one species of *Carphephorus* the same biseriate gland was accompanied in the depression by uniseriate but non-capitate glandular trichomes while in all four species of *Carphochaete* the same grouping occurred but the biseriate gland was different in form.

5. In the other species of *Carphephorus* uniseriate glandular trichomes were depressed either singly, in one species, or grouped, in two others.

6. The two other species of *Trilisa* were characterized by compact, depressed, uniseriate, secretory glands.

7. The small uniseriate capitate glands were observed only on species of *Kuhnia*.

8. As the punctate condition results from a depressed gland or glandular trichome it was found in all genera and all species except *Trilisa odoratissima* and *T. paniculata*.

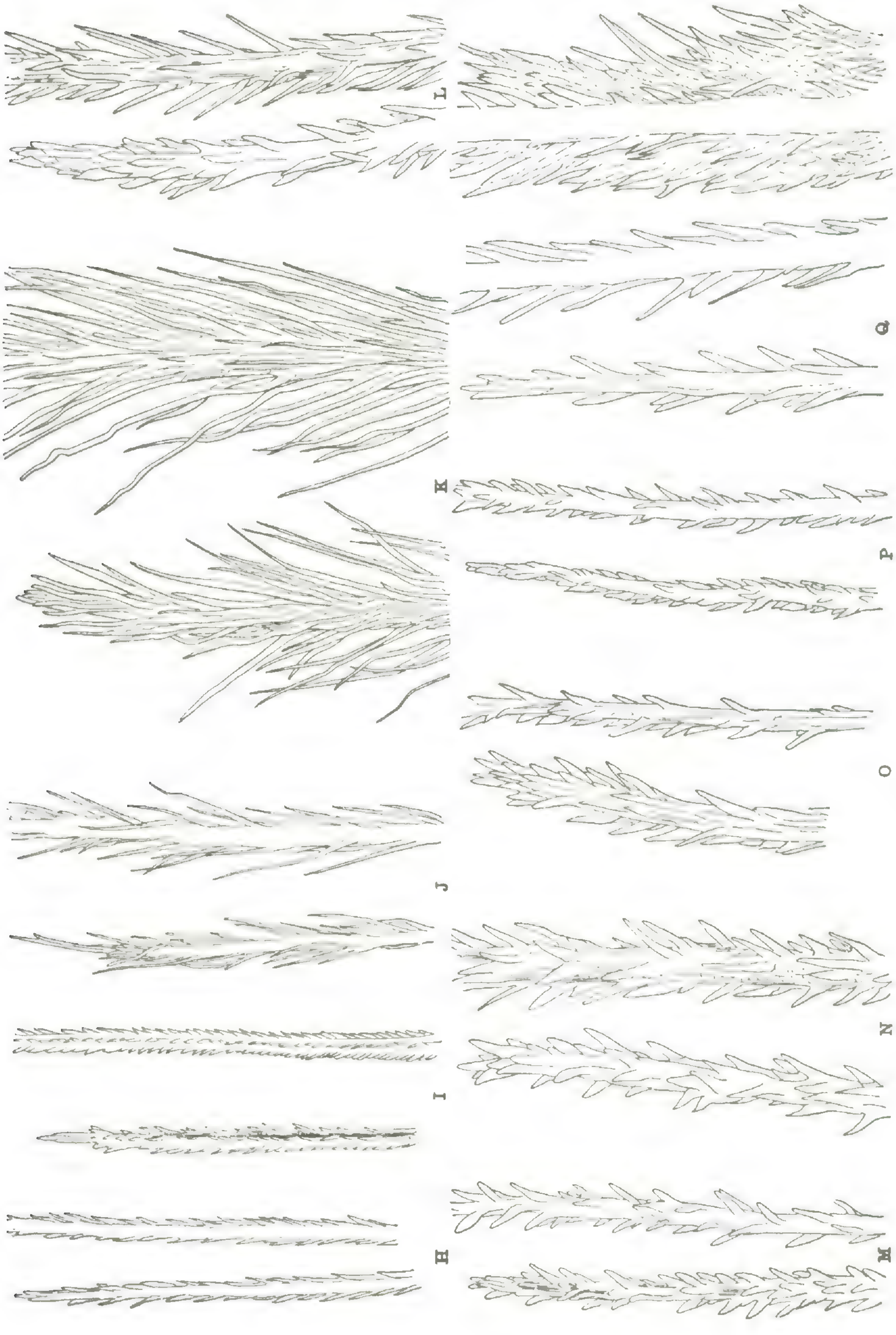
9. While in representatives of each genus, the depression contained the biseriate glandular trichomes, in three species of *Carphephorus* there were uniseriate trichomes singly or in groups. Thus the punctate condition accompanies different glandular contents in these genera.

A very reticulate pattern is evident in the distribution of the glandular trichomes. Though some form is found in every species, the same is not necessarily common to all those of any genus.

IV. Pappus

In the key to his treatment of this group of genera, Hoffmann (1890) made use of differences in the length of barbules of the pappus, besides the singular scale-like nature of that of *Carphochaete*. Thus *Kuhnia* was distinguished by plumose pappus from *Brickellia* and *Barroetea*. Illustrations of *Kuhnia eupatorioides* and *Brickellia californica* A. Gray (Fig. 81 B & C) were drawn to scale and indicate that for these two species, the barbules of the former are at least four times as long as the latter.

Robinson made little use of the pappus in the classification of *Brickellia* because he found that as well as in barbule-length, the number of setae varied widely from species to species. As pointed out (Gaiser 1953), Robinson did include its plumose nature under the sectional heading of *Steviastrum* and elsewhere only in the species-descriptions of *B. brachyphylla* and *B. monocephala*. Lactic acid mounts have confirmed a wide variation in the length of barbules of more than six times from these two



FIGURES OF PAPPI

which are the longest, to the shortest. Generally in any species the barbules become a little longer away from the tip of the seta. However, their arrangement in this genus seemed distinctive from that seen in *Liatris*. The generally flattened appearance along the greater length of the seta in many species resolved itself as a distichous arrangement of the barbules along the axis, as shown for *B. Nelsonii* Robinson (Fig. H). In other species, e.g., *B. Coulteri* where the barbules were only about half as long, their arrangement along the mid-portion of the seta approached the marginal appearance of the serrulate-paleaceous type of Small (1919, fig. 17H). However, the central axis in all the specimens seen did not broaden greatly, showing an increase in diameter of not more than twice with an elongation of barbules of three times or more than that amount. *Brickellia diffusa* and *B. filipes*, the two annuals, appeared exceptional in having the barbules arranged in three rows or tristichously. Always at the apices, the barely emerging barbules came in less regular arrangement and for this reason the illustrations include an apical as well as a median portion of a seta. In some species having short barbules, the irregularity persisted further along the axis.

Comparison of similar mounts of species of all of these genera here studied was therefore included. In contrast to the very large genus *Brickellia*, the smaller genera showed a greater uniformity in the nature of the pappus.

In *Barroetea* the length of the barbules varied little in the six species examined, being about equal to the shortest in *Brickellia*. Their arrangement also was uniform so that the seta had the appearance of a four-angled structure, due apparently to a tetrastichous arrangement of the barbules. In figure I, the row of barbules in the center below were not included. No exact equivalent for this was found in Small's figure 17 of pappus forms in the *Compositae*.

The plumose pappus of species of *Kuhnia* varied distinctly from *Barroetea* not only in the length of the barbules but also in the longer spaces between the points of their emergence from the axis and in their flat, distichous arrangement (Fig. J). In the latter they resembled *Brickellia*. In comparison with the plumose pappus of a species of *Liatris* (Fig. K) the barbules are slightly more slender and appear much less abundant because they do not extend from the mid-axis. Although the tips of emerging cells can be seen over the center region, they do not project laterally.

EXPLANATION OF FIGURES OF PAPPUS

All figures are of pappus from specimens in the Gray Herbarium and will be referred to by the collector's number, except Figs. M and N, *Trilisa paniculata* and *T. carnosa* which were of accessions studied cytologically, from Sebring, Highlands Co., Fla., Ray Garrett, Nov., 1948.

Fig. H. *Brickellia Nelsonii*, Nelson 4449. Fig. I. *Barroetea brevipes*, Nelson 1520. Fig. J. *Kuhnia adenolepis*, Pringle 2933. Fig. K. *Liatris squarrosa* var. *glabrata*, Rydberg 1505. Fig. L. *Liatris ligulistylis*, Nelson 1651. Fig. O. *Carphephorus tomentosus* var. *Walteri*, Fernald and Long 11173. Fig. P. *Garberia heterophylla*, Nuttall. Fig. Q. *Carphochaete Schaffneri*, Schaffner, 241.

The author is greatly indebted to Dr. B. G. L. Swamy for these figures, drawn × 45.

This is indicated in another illustration of *Kuhnia eupatorioides* (Hoffmann 1889, Fig. 60D) where it can also be compared with *Liatris pycnostachya* Michx. (Fig. 60B), which has a barbellate pappus. At least five of the seven species of *Kuhnia* had barbules of approximately the same length, while those of *K. leptophylla* var. *maxima* and *K. adenolepis* were from half to three quarters as long. In length the barbules of this majority are somewhat intermediate between that of *Liatris squarrosa* (L.) Michx. var. *glabrata* (Rydb.) Gaiser, belonging to section *Euliatris* with plumose pappus and *L. ligulistylis* (Nels.) K. Sch., of section *Suprago* in which it is barbellate.

While it is difficult, when the barbules are as long and as abundant as in the plumose pappus of *L. squarrosa* (Fig. K) to illustrate their points of emergence even at the apex, when they are shorter as in the barbellate type of *L. ligulistylis* (Fig. L), their general disposition all around the axis is evident. This is similarly shown in the figure of *L. pycnostachya* of Hoffmann (l.c.). The projecting barbules are not limited to two sides and give no suggestion of a flattened appearance. They emerge somewhat spirally as shown also for this type (Small fig. 17D). This same arrangement was seen in the mounts of species of *Trilisa* (Figs. M & N), *Carphephorus* (Fig. O) and *Garberia* (Fig. P) all of which have barbellate pappi with barbules shorter than those of *Liatris ligulistylis* though equal to those of some other species, e.g., *L. gracilis* Pursh. Except for slight variations in the length of the barbules, the similarity of the pappus from genus to genus, as well as of the species within a genus was too great to allow any differences of classificatory value for *Trilisa, Carphephorus* and *Garberia*.

Of course, *Carphochaete* with its paleaceous pappus is quite distinctive from all the others (Fig. Q). It is dilated and scale-like at the bottom and for this reason the figure of this form includes a basal portion in addition to the median and apical. *Carphochaete Schaffneri*, the species illustrated, has the shortest free barbules at the apex of any of the four. The two other Mexican species are very similar to it, while in *C. Bigelovii* they are almost twice as long.

DISCUSSION

This study of six genera indicates a relationship with the two others previously studied, *Brickellia* and *Liatris*. With the exception of *Kanimia*, of which it has been impossible to include cytological examination and therefore discussion has been omitted, there is support for the taxonomic grouping of the subtribe *Kuhniinae*. *Kanimia* will have to be compared cytologically with *Mikania*, the genus of the previous subtribe *Ageratinae*, with which it may well be a connecting link because of the several technical characters which the two genera have in common.

Furthermore, some points of relationship within the subtribe have been

added to those noted by earlier authors. These have served as a guide in the preparation of a key (see p. 124) which attempts to more nearly approach a natural classification. It has already been pointed out that when Cassini established each of the two new genera, *Carphephorus* and *Trilisa*, he placed them next to *Liatris*. Also because of the strong similarity of the flowers, Nuttall first described *Garberia* as a shrubby *Liatris*. With the additional evidence gained from the study of seedlings, trichomes, pappi, and chromosome numbers, it is proposed to refer to these four genera as Group I.

Likewise there is sufficient evidence to warrant a second grouping. When Gray (1879) established the genus *Barroetea*, he began the description "Involucrum (15–25) flores *Kuhniae* et *Brickelliae*." Hoffmann (1890) in his introduction to the subtribe also referred to *Barroetea* as approaching *Brickellia* in all else except the nature of the fruit. Robinson, who monographed both these genera, re-emphasized their strong similarity in habit and involucre, giving the flattened achene and sharply toothed leaves as the chief points of difference. To separate *Kuhnia* from *Brickellia*, the same author referred to its less strongly imbricated phyllaries and plumose pappus. For Shinners (l.c.) these technical characters were not completely satisfactory, as was also an additional one, the nature of the root system. His conclusion was that though separately imperfect they were "strengthened by the obviously close relationship of the species of *Kuhnia* to each other, making a closeknit and recognizably distinct group." The association of these three genera will be continued as Group II.

Even in the seedling stage, at least as they grew in the greenhouse, differences were noted which distinguish the two groups. Those of species representing Group I, had a rosette of leaves which persisted without production of a flowering stem for a longer period than would necessarily be required for a biennial. In seedlings of *Garberia*, the one shrub of the group, this stage did not last as long and then a central leafy stem began to appear though it never flowered. However, species of Group II, including representatives of all three growth-forms, e.g., annual herb, perennial herb, and shrub, produced elongating central axes almost at once and these flowered before the end of a year. The seedlings of *Carphochaete Bigelovii* resembled the members of this latter group.

It was felt by Shinners that in distinguishing *Kuhnia* undue reliance had been placed on the plumose pappus because it might not be the exclusive type of a genus, e.g., *Liatris*. From an examination of the pappus of these genera by lactic acid mounts, it was found that the arrangement of the barbules differed in these two. Further, though the barbules were longer in *Kuhnia* than in species of *Brickellia*, their lateral arrangement was more nearly like the distichous pattern found in the majority of the species of that genus. In two species of *Brickellia*, the three-sided or tristichous arrangement suggested a mid-way condition between that of the others and that typical of *Barroetea* where it was four-sided or tetra-

A GENERIC KEY TO THE KUHNIINAE [7]

Anther apex having an ovate or oblong membranaceous appendage, achenes 10–20 (rarely 6–9) ribbed, phyllaries indefinite in number.

(a) Pappus squamiform, dilated at the base, small shrubs, leaves opposite, young plants without rosettes, corolla rose-colored or white, chromosome number n = 11 **Carphochaete.**

(a) Pappus setose.

(b) Phyllaries not conspicuously striate, leaves alternate, young plants with rosettes, corolla rose-colored, rarely white, barbules of pappus indefinitely arranged along the axis, chromosome number n = 10 . . . . . GROUP I

(c) Woody shrubs, leaves alternate obovate, rosette-form not persisting long, phyllaries herbaceous, pappus barbellate . . . . . **Garberia.**

(c) Perennial herbs, leaves linear to lanceolate, rosette-form persisting.

(d) Receptacle chaffy, phyllaries subequal pappus barbellate . . . . . **Carphephorus.**

(d) Receptacle naked.

(e) Plants arising from thickened fibrous root-system, phyllaries 2–3 seriate pappus barbellate . . **Trilisa.**

(e) Plants arising from a corm-like or deeply penetrating root-system, phyllaries imbricate, herbaceous or colored or scarious, pappus barbellate or plumose . . . . . **Liatris.**

(b) Phyllaries thin, striate, scarcely herbaceous, leaves alternate or opposite, young plants without rosettes, corolla ochroleucous to yellow, rarely rose-colored, barbules of pappus tend to be in linear arrangement along the axis, chromosome number n = 9 . . . . . GROUP II

(f) Achenes prismatic or rounded.

(g) Phyllaries imbricate in several series, shrubs and perennial, rarely annual, herbs, pappus tends to be arranged distichously, rarely tristichously **Brickellia.**

(g) Phyllaries 2–3 seriate, perennial herbs from long conical roots, pappus plumose, barbules arranged distichously . . . . . **Kuhnia.**

(f) Achenes compressed, annual and perennial herbs, barbules of pappus arranged tetrastichously . . . . . **Barroetea.**

stichous. Thus in the pappus of the two smaller genera, in comparison with *Brickellia*, the arrangement of barbules alone differentiates *Barroetea*, and arrangement in addition to length, *Kuhnia*. While interspecifically *Brickellia* shows considerable variation in length of barbules, the species have the same basic linear arrangement which adds support to the placement of these three genera in one group. Similarly the four genera of Group I resemble one another in a less definite, somewhat spiral arrangement of the short barbules as is shown in figures of setose pappus.

In addition to the characters in prevalent use by taxonomists, it has been noticeable that in the *Eupatorieae*, it was necessary to pay consider-

[7] Exclusive of *Kanimia*.

able attention to glandular structures. Robinson had established species as well as varieties on the presence of glands on the phyllaries, e.g., *Kuhnia adenolepis*, *Brickellia adenocarpa* var. *glandulipes*, etc. Likewise Brandegee (1908), who described two of the seven species of *Barroetea*, found *B. glutinosa* "differing from the others of the genus" because of the glandular leaves. Also, the common use in manuals, as well as descriptive treatises, of the term punctate and puncticulate in some species, left open the question of general application for all of each genus. As explained under *Brickellia*, there was the need for interpretation of the overlapping use of the various terms applied to the depressed glands and the punctate condition. A more detailed comparison than had been possible by macroscopic examination, has helped to clarify.

From the reticulate pattern of glandular trichome distribution in six genera, summarized in Table III, and of *Brickellia* (Table III, Gaiser 1953), it was seen that some form was represented in each species. *Liatris* also can come in this inclusive statement. In the introduction to the treatment of that genus, it was stated that small sunken resinous glands were generally found in the leaves of species. Examination of cleared leaves of at least several species have given confirmation of the presence of the depressed biseriate trichome in connection with the punctate condition, as shown for *L. punctata* (Figs. 74, 75). A closer analysis of these tables gives indication of some intergeneric similarities.

In several species of *Brickellia*, the pubescence consisted almost entirely of the biseriate glandular trichome. That, of all the species of the other five genera examined, only puberulence of one species of *Barroetea* was composed of this form, is another point to add to the number in which that genus strongly resembles *Brickellia*. However, in the thick leaf of *Brickellia glutinosa*, a similar shorter biseriate trichome was shown to make up the depressed gland which gives a surface appearance of only two hemispherical cells as seen in species of *Kuhnia*, as well as the other species of *Barroetea* and *Brickellia*. The conclusion was reached from the range of variation seen in the extent to which the biseriate gland rose above the surface in different species of *Brickellia*, that the superficial glandular trichome was an elevated expression of the depressed gland. With the additional evidence in the fleshy leaves of the other genera of the heights it may attain and still remain macroscopically subsurface, there is no reason to doubt the generality of the statement. It is as understandable that the height of this small organ should vary in leaves of different species as that non-glandular trichomes should vary in length. More important than the variation from a depressed to an elevated condition may be the uniformity of this biseriate glandular organ. While these three genera of Group II have in common this single, similar content in the depressions in the epidermis of the leaf, the four genera of Group I have mixed contents of biseriate and uniseriate, grouped or single uniseriate, or single uniseriate without correlation to the punctate condition.

Examining this apparent diversity, there is a link with the previous three genera in *Garberia* and one species of *Carphephorus* having this

same biseriate form in the grouping along with the uniseriate. To these, the other *Carphephorus* are tied in having only uniseriate trichomes and *Carphochaete*, in having uniseriate with a different form of biseriate trichomes. Likewise in the two species of *Trilisa* the uniseriate trichome, though not accompanied by leaf punctation, appears similar in form to the depressed of *Carphephrous bellidifolius*, while *Trilisa carnosa* has the depressed biseriate resembling those of Group II. Thus while there is greater uniformity in the three genera of Group II, those of the other group seem to have a similitude in intra-generic variations. The particular form of the biseriate depressed gland of *Carphochaete* is individual among them. While its difference sets it apart from the genera of both groups, the true significance of this variation may be better understood when further knowledge is obtained of the forms in the many genera of other subtribes.

Further emphasis on relationships by glandular structures in these genera was found in the fact that there was a smaller, uniseriate, capitate trichome, which would not be readily observed without a microscope, along the veins and under surface of leaves of species of *Brickellia*. The only other genus of the subtribe studied to which it has been found common is *Kuhnia*. A slightly enlarged form apparently became the specialized type of *K. adenolepis*.

From a consideration of the non-glandular trichomes [8] the largest genus has the widest variety. Comparable preparations of other genera contributed no distinctly new type, though in *Carphephorus*, *Trilisa*, and one species of *Kuhnia*, they were more nearly uniform in diameter and tapered a little less than the attenuate form shown for *Brickellia*. That all the types seen in that genus were not represented in the smaller genera could be explained probably by the smaller total of species. However, in *Brickellia* considerable variation was found in the size of chromosomes and in some subsections a correlation with the types of trichomes.

Cytological evidence has been obtained of some species of each of the genera of the *Kuhniinae* except *Kanimia*. Though incomplete, it supports the conclusions obtained from other sources. The basic number of chromosomes is 10 in the four genera of Group I, 9 in the three genera of Group II and 11 in *Carphochaete*. While no other genus of the subtribe has the same number as *Carphochaete*, the fact that the three basic numbers vary only by one, may be taken as further indication of a fairly close relationship of the members of this subtribe. This seems more significant when the number of species examined for the several genera to which the same number is common, totals forty-seven with n = 9, and thirty-nine with n = 10. Of course these two chromosome numbers are represented many times in genera of the Compositae as can be seen in Darlington and Ammal (1945, p. 220) where the basic numbers of the tribes of the Compositae are given. When turning to the reports for the tribe *Eupatoricae*, of which there have been few so far, the number 11 does not appear. The recent addition by

[8] Gaiser (1946) in referring to pubescence as being of little use for species differentiation in *Liatris*, had not made microscopic analyses and there has not been time as yet to do so for that genus.

Grant (1953) of numbers for at least thirty-two species of *Eupatorium* from the temperate zone, give 10 and 17 as the lowest numbers, and 9 for one tropical species of *Vernonia*. The number 11 does not appear. This does present a challenge to investigate *Kanimia*. Also it raises the question of possibly finding the same number in a genus of another subtribe which perhaps may show further intertribal relationships with *Carphochaete*.

Of two species of *Mikania*, the genus of the previous subtribe *Ageratinae*, which has characters in common with *Kanimia*, it was possible to obtain some seeds (see Table I). The somatic chromosome number of three accessions of *Mikania scandens* Willd. and one of *M. cordifolia* (L.) Willd. was found to be 2n = 38 (Fig. 21), which is quite different from that in any of the *Kuhniinae* investigated. Thus it seems quite probable that cytology might give the deciding evidence for or against the segregation of these two genera within the same subtribe.

No lower basic number was found among these genera than had been found in *Brickellia* and *Liatris*, or had been known previously among the *Eupatorieae*. These numbers, 9 and 10, are higher than have been found in a number of the other tribes of the Compositae, e.g., *Chichorieae* with 3, *Heliantheae* and *Astereae*, with 4, *Inuleae* and *Senecioneae* with 5, etc., but this may find its explanation in the few genera studied. Of the *Kuhniinae*, the genera of Group II with Mexico as their geographic center of distribution, have the lower number 9, while those of Group I, which are to the north of the Mexican boundary have 10. At this time there is no evidence of the origin of these divergent genetic lines. So far, the most northerly genus, *Liatris*, and in that only the *Punctatae* series, remains the only one in which polyploidy has been found. The tetraploid, *L. punctata*, reaches the most northerly latitude of any species of that or any other genus of the subtribe and so exemplifies Hägerup's theory. Since the same species reaches the southern extremity of the range for the genus along the mountains and the diploid is found on the plains in between it also provides an example of the polyploid occupying a wider area than the diploid. Müntzing (1936) believes that the extensive range is the combined result of polyploidy and polymorphism which has enabled adaptation to a wider range of habitats some of which may be unfavorable. Of all the other genera of the *Kuhniinae* few include any species of very extensive range and none which is exactly comparable to *L. punctata*. *Kuhnia eupatroioides* is the only polymorphic species of that genus, occurring in the central states from the northern to the southern boundaries, Michigan to Texas, and from Kentucky to Montana in the west. In his introduction, Robinson referred to *Brickellia grandiflora* and *B. californica* as the two most widely distributed and variable species. Both were found to be diploid in these studies which included a generous representation of thirteen accessions of the latter species. The former species like two others studied, *B. microphylla* and *B. oblongifolia* reach the northern limit for that genus in Washington State, but they also were diploid.

Excepting the species of *Brickellia* in Brazil, the most southerly one from Costa Rica, *B. argyrolepis*, was also a diploid. For the discussion

of the polyploid complex and tropical plants, as pointed out in the introduction, this genus is somewhat exceptional since though within the tropical latitudes the species live on higher altitudes. Of *Barroetea*, which at similar altitudes does not extend north of Mexico, neither of two species were polyploid. Also one speices of *Kuhnia* from the southerly limits for that genus was diploid like the three congeners from the United States. The conclusion from this discussion still remains that for these closely related genera, as they have been represented from Central America northward, polyploidy was not prevalent and occurred only in the most northern genus of Group I. However, variation in the size of the chromosomes was noticeable and the karyotypes of the shorter units occurred only in the genera of the more southern group.

This does not mean that we should not expect polyploidy in genera of the tropics. For comparison, in the tropical genus *Anthurium*, of which thirty-seven of four hundred and eighty-six species (Engler 1905) were examined from plants as they grew mostly in the New York Botanical Garden, the situation is quite different. While many additional species have also been added since Engler's monograph of the genus, there is indication that polyploidy is not singular and occurs in species of both limited and wide distribution (Gaiser 1927). With 30 as the lowest somatic number found, at least two other numbers of a polyploid series were represented, two species with ca. 50 and three with ca. 60. The five polyploids were distributed to as many different sections, some nearly monotopic and others, the largest of the genus, e.g., *Urospadix* with ninety-five species. *Anthurium radicans* which belongs to the section, *Chamaerepium*, comprising two species, is limited to east Brazil, and *A. Wallisii* of section *Polyneurium* of thirty species had been reported as having been collected only once in Colombia. In comparison with tetraploid *A. crassinervium*, from Venezuela, Colombia, Panama, and Tobago Island, nine other diploid species of the second largest section *Pachyneurium* with fifty species were found to be fairly restricted. Two species of section *Urospadix*, very similar to the polyploid *A. digitatum* from Venezuela and Tobago Island, had been collected from comparable areas. However, the fifth, *A. scandens*, is the most variable species in the genus, including five varieties and is known in one of its forms wherever Anthuriums grow. With even but fractional representation studied cytologically, all the complexities of polyploidy in percentage of incidence, different multiples of numbers and correlation of geographic distribution occur in that genus. Also, since Grant (l.c.) found fifteen polyploids (almost fifty percent) among the northern Eupatoriums examined, others might be expected among the many more tropical species of that large genus.

While the studies of *Liatris* were of a different time and were not all accompanied by exactly comparable photographic figures, chromosomes of the series *Spicatae* (Gaiser 1949) were considered to be the longest and to show greater variation than those of the series *Graminifoliae* (ibid. 1950a) and *Punctatae* (ibid. 1950b). Reference to the analysis of the morphology of the chromosomes of *L. pycnostachya* (1949 p. 127) gave

two pairs of long chromosomes in the karyotypes of 2 Lm, 2 Lst, 4 Mm, 4 Msm, 2 Mst, 4 Sm, 2 Sst. In the more recent comparisons the few species of the smaller genera of Group I varied little if at all from species to species. Also, the generally similar karyotypes of *Trilisa* and *Carphephorus*, including three pairs of long chromosomes, were found to vary somewhat from *Garberia* only in the types of the short and medium chromosomes. By comparison, *Carphochaete Bigelovii* was the only species to have a greater number of long chromosomes, four pairs rather than three.

Brickellia with the greatest number of species, had a great variation in chromosome sizes. Of thirty-four species in which the karyotypes were carefully analyzed, nine had only short and medium chromosomes, while in all the others there were also long ones. From the analyses of species of all these genera, only those of *Kuhnia* and *Barroetea* had such a karyotype of the two classes of shorter units. Thus not only have these three genera the same number in common but like a minority of the species of *Brickellia*, the species studied of the two smaller genera, have chromosomes representing an amount of chromatin less than is found in any of the others.

While too few species of *Barroetea* have been examined to draw conclusions regarding that genus, more than half of those of *Kuhnia*, including all but one variety of the polymorphic species *K. eupatorioides* have been included. The great homogeneity in the karyotype as well as chromosome number for all of these, shows a genetic basis for the close relationship of species of *Kuhnia* to each other, pointed out by Shinners. By contrast the great diversity in chromosome length found in species of *Brickellia* accompanies a diversity of growth from woody shrubs to herbaceous annuals. None of the genera of Group I can compare with this. In *Liatris*, the largest of them, all the species are herbaceous perennials of a fairly similar type.

In the discussion of *Brickellia*, it was pointed out that a minority of the species examined, nine out of thirty-four, had a complement of shorter chromosomes. The species at the opposite extreme having the longest chromosomes, *B. monocephala* and *B. grandiflora*, were considered by reason of their modified underground structure, etc., as belonging to a specialized group of that genus. Others next to them, also having a greater total of chromatin material by reason of longer chromosomes than in the major group, included shrubs and herbs native to Costa Rica, Guatemala and Mexico. With the most woody species from Costa Rica among these, and the one annual examined, in the first group, there was some ground for considering that evolution had gone on in conjunction with reduction in chromatin in that genus. It is of interest therefore that the only other genus including annuals, *Barroetea*, also had short chromosomes in the two species examined. The genus includes no true shrubs and only one perennial variety of a species that has been described as being somewhat woody at the base. *Kuhnia*, too, is a genus consisting entirely of perennials and in it there was found a similar karyotype of the two shorter classes of chromosomes. While it is impossible to trace the steps of evolution from

one genus to another with certainty, it is indicated from the present evidence that the direction at least, was from *Brickellia* to the two other genera through some form, not necessarily extant today, having a complement of shorter chromosomes. Whether this happened in two successive steps or at one time remains a question also. The fact that both genera still include few and, for the most part, less variable species indicates that they are more recent than *Brickellia*. The repeated reference to the close similarity of *Barroetea* and *Brickellia*, especially as seen in both including annual species, suggests that there are possibly blocks of genes common to these two and this could have been one mutation. Also the indecision regarding basic differences between *Kuhnia* and *Brickellia* gives weight to the probability that this might have come as another step. The similarities of each of the two smaller genera to *Brickellia* appear closer than the interdependence of all three. Yet, as has been pointed out, from karyological studies, the six species of *Kuhnia* and two of *Barroetea* had karyotypes consistently represented by a pair of satellite chromosomes. Only in three, of about half of the species of *Brickellia* examined, was this type of chromosome regularly visible. Two of these were xerophytes, *B. incana* and *B. Greenei*, very restricted in distribution and remarkable for their large heads and seeds which are distinctive. The third was *B. Coulteri*, from Baja California, the only species examined of subsection *Brachiatae*. Most of the other seven species have been reported but once and from widely separated regions in Mexico and certainly should be compared cytologically. Without complete representation of a genus, the species not studied may be the ones which withhold the most significant truths. Perhaps the best that can be expected is to gain at least a point of vantage from which to envision the horizons for further efforts in a project.

It is difficult to extrapolate true phylogenetic relationships within Group I. In all four genera the karyotype is made up of more closely approximating units than were seen within the one genus *Brickellia*. Some variation has been reported in the species of five series of the genus *Liatris*[9] but is not as striking as has been found in *Brickellia*. There was no evidence of marked morphological changes or reduction in size of the chromosomes. Also there is a general similarity of karyotype in the two smaller genera *Trilisa* and *Carphephorus*, including three pairs of long chromosomes. From these, *Garberia* was found to vary only in the medium and short chromosomes. Likewise, except for this one shrub *Garberia*, there is a greater homogeneity in the growth-form represented by each of the three genera. They are herbaceous perennials, provided with excellent modified storage rootstocks, mostly corm-like in *Liatris* and more tuberous in *Trilisa* and *Carphephorus*. From the discussion pertaining to growth-forms in *Brickellia*, just such as these were considered to represent a form of specialization and, these may very well be from a more primitive type now extinct. In the one living species of *Garberia* may lie

[9] A chromosome list will shortly be forthcoming for species of the other series except the *Squarrosae*, which Dr. Pauline Snure will contribute.

the hint of another more woody progenitor for the other three genera.

The dissimilarity of the karyoytpe of *Carphochaete Bigelovii* to the species of Group I lay in the fact that it was the only species to have two additional chromosomes, four long chromosomes instead of three and three short ones rather than two. These factors contributed to its having the greatest content of chromatin in any of the genera studied. Comparison of it with the unusually long chromosomes of *Brickellia monocephala* (see Fig. 30, Gaiser 1953) is favorable except for the extra pair of chromosomes. The singularity of its karyotype, supported by the distinct form of the biseriate depressed gland and the individuality of its pappus, is sufficient to set it apart from the genera of both Groups I and II. Yet the prime reason for its inclusion in the subtribe *Kuhniinae*, the similarity of its anther and achenes, also gains weight in a proximal chromosome number and karyotype to that of Group I and in the actual presence of a depressed biseriate gland.

Without examining other genera having paleaceous pappi for comparison with *Carphochaete*, it would be premature to generalize on the evolution of pappus forms. That this small group of related genera may contribute to the overall study is indicated by the variety shown in the barbule-arrangement especially in the three genera of Group II. In *Barroetea* and *Kuhnia* there is near uniformity for the species of each genus, while in the more numerous species of *Brickellia* there is a variety of almost imperceptible changes. The general tendency is for a flattened, lateral arrangement of barbules in two rows. While the significance of their quadrate, linear arrangement in *Barroetea* is not clear, it may be but one of nature's experiments and so also the tristichous disposition in *Brickellia diffusa* and *B. filipes* may be a further shuffling of genes. However, since the latter species are annuals and since *Barroetea* is the only other genus including annual species, it would be in agreement with phylogenetic evidence to assume that the change in *Brickellia* was in the direction away from the flat or distichous arrangement. And if so, the latter referred to as bearing a marginal resemblance to the serrulate-paleaceous, could have been derived from the paleaceous or more foliar by reduction. This would be in agreement with the conception of Babcock and Stebbins (1937) for genera of the *Cichorieae* rather than the alternative hypothesis of Small (1916), that the paleaceous types result from the fusion of the simple scabroid setose which constitute the primitive type.

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MISCELLANEOUS MALAYSIAN NOTES

E. D. MERRILL

With one plate

MORACEAE

Ficus porteana Regel, Gartenfl. 11: 280. *t. 372*. 1862; Gagnep. in Lecomte, Fl. Gén. Indo-Chine **5**: 774. 1928.

Ficus malunuensis Warb. in Perk. Fragm. Fl. Philipp. 196. 1905; Elm. Leafl. Philipp. Bot. **1**: 192. 1906; Merr. Enum. Philipp. Fl. Pl. **2**: 56. 1923.
Ficus cordatifolia Elm. Leafl. Philipp. Bot. **4**: 1250. 1911.

My attention was called to *Ficus porteana* Regel by Gagnepain's reference of certain Indo-Chinese material to it and by his reduction of *Ficus malunuensis* Warb. to it as a synonym. Regel's species, entirely overlooked by me when engaged in the preparation of the Philippine enumeration, was based on specimens cultivated in Moscow, grown from seeds secured by Mr. Porte in the Philippines (Luzon) in 1861. Regel's description is based on sterile material and from his figure, a somewhat juvenile form, for the large leaves are shown as having a fairly large lateral lobe on each side, a character that is lost in mature specimens. There is not the slightest doubt as to the identity of Warburg's species, also based on Luzon material, with the form characterized forty-three years earlier by Regel. There is some doubt in my mind as to whether or not the Indo-Chinese specimens referred here by Gagnepain actually represent the same species as the Philippine form. Its general alliance seems to be with *Fictus callosa* Willd.

FICUS PYRIFOLIA Burm. f. Fl. Ind. 226. 1768 = **Pyrus pyrifolia** (Burm. f.) Nakai, Bot. Mag. Tokyo **40**: 564. 1926; Rehd. Man. Cult Trees Shrubs ed. 2, 404. 1940.

This reduction was made on the basis of an examination of Burman's specimens in the Delessert herbarium at Geneva; there are three sheets, all sterile, from the vicinity of Nagasaki, collected by Kleinhof; these, according to Nakai, represent the ordinary Japanese sand pear, which by various authors has been placed under *P. sinensis* auctt., *P. serotina* Rehd., and *P. montana* Nakai. Nakai attempted to define a number of minor forms of this cultigen, but no botanist has, as yet, clarified its relationships with the Chinese forms of the sand pear. In my treatment of Burman's species, Philipp. Jour. Sci. **19**: 346. 1921, working solely from Burman's descriptions, I suggested that *Ficus pyrifolia* Burm. f. might prove to be the same as *Ficus erecta* Thunb., the type of which was from Japan, but this is an error. In recent years the Burman name has been attached to some Chinese collections of *Ficus erecta* Thunb.

URTICACEAE

Laportea peltata Gaudich. Freyc. Voy. Bot. 498. 1830, *nomen nudum*, et ex Decaisne, Herb. Timor. Descr. 162. 1835, *descr.*; Wedd. Arch. Mus. Hist. Nat. 9: 126. 1856 (Monog. Urt. 126), et in DC. Prodr. 16(1): 80. 1869, cum syn.; J. J. Sm. ex Koord. & Val. Meded. Dep. Landb. 10: 678. 1910 (Bijdr. Boomsoort. Java 12: 678); Koord. & Val. Atlas Baumart. Java 4: *fig. 796*. 1918.

Urtica peltata Blume, Bidjr. 496. 1825.

MINDANAO: Cotabato, Nutol, *Bur. Sci. 84935, 84941, Ramos & Edano*, March, 1932, a tree 8 m. high in rather dry forests at low altitudes. Java, Timor, and probably in other parts of the Malay Archipelago; new to the Philippines.

Both of the above cited specimens agree very closely with authentically named Javan specimens collected by Koorders, one having been distributed as representing the very different *Laportea crassifolia* C. B. Rob., and the other as *L. mindanaensis* Warb. It seems to be apparent that Gaudichaud did not know of the published description of *Urtica peltata* Blume, Bijdr. 496. 1825, for his original publication of the accepted binomial was simply a *nomen nudum* and a new name for *Urtica atrox* Leschen., also a *nomen nudum*. Therefore the authority should not be cited as "(Blume) Gaudichaud," but merely as Gaudichaud. The first description of the species under *Laportea* was that prepared by Decaisne, and he also cited only *Urtica atrox* Lesch. as a synonym. Weddell in 1856 first, and apparently correctly, associated Blume's earlier name with that so casually published by Gaudichaud and later validated by Decaisne.

Laportea elliptica sp. nov.

Laportea peltata sensu Merr. Univ. Calif. Publ. Bot. 15: 50. 1929, non Gaudich.

Species *L. peltatae* Gaudich. affinis, differt foliis majoribus, ellipticis, haud molliter pubescentibus sed subscaberulis et secus costam nervosque pilos urentis numerosos ferentibus, nervis primariis utrinque circiter 15. Arbor, trunco 30–45 cm. diametro, ramulis ultimis plus minusve incrassatis, siccis circiter 8 mm. diametro, pubescentibus, cicatricibus ad 8 mm. diametro notatis, partibus junioribus dense subadpresse hirsutis; foliis longe (8–13 cm.) petiolatis, perspicue peltatis, basi late rotundatis, ellipticis vel subobovato-ellipticis, chartaceis, 15–30 cm. longis, 11–15 cm. latis, apice breviter acuminatis, margine breviter dentatis vel denticulatis, dentibus inter se 1.5–3 mm. distantibus, siccis olivaceis, supra minute albido-verruculosis, secus costam pubescentibus et pilos urentis ferentibus, subtus scabridulis, paullo pallidioribus et nervis reticulisque exceptis glabris vel subglabris; nervis primariis utrinque circiter 15, perspicuis, subtus elevatis, curvato-patulis, secus marginem arcuato-anastomosantibus, reticulis distinctis, elevatis et cum costa nervisque plus minusve pubescentibus et pilos brevis numerosos urentis ferentibus; inflorescentiis longis, laxis, paniculatis, usque ad 45 cm. longis, plus minusve pubescentibus et pilis

numerosis urentibus instructis, ramis primariis 4–8 cm. longis; floribus ♀ sessilibus, in ramulis ultimis brevibus flabellatim dispositis, sessilibus, capitulis 5–9-floris, calycis segmentis acuminatis, vix 0.5 mm. longis; acheniis compressis, glabris, subovatis, 2 mm. longis, acuminatis, stylis persistentibus gracilibus, ad 3 mm. longis, leviter patule hirsutis; floribus ♂ numerosis, calycis segmentis subellipticis, 1.5–2 mm. longis, filamentis 3 mm. longis.

BRITISH NORTH BORNEO: Tawao, *Elmer 21472* (♀), *11433* (♂), October 1922 to March 1923.

When the Elmer collections were being studied at the University of California, these specimens were referred, on the basis of published descriptions only, to *Laportea peltata* Gaudich, and were reported as such; but it was then noted that they differed from Gaudichaud's species in certain striking characters. Now that it is possible to make direct comparisons with authentically named Javan specimens of the Koorders collections, it becomes evident that there is really little in common between this Bornean form and *Laportea peltata* Gaudich., except in the conspicuously peltate leaves of both. The indumentum of the two species, as well as the leaf shape and size, and the more numerous lateral nerves in the present species are very different. In Gaudichaud's species the lower surface of the leaves is very densely and softly cinereous-pubescent, the indumentum entirely covering the parenchyma; in *Laportea elliptica* the midrib, and to a limited degree the nerves, are pubescent, but these and the reticulations bear many short, stiff, stinging hairs; yet the parenchyma within the ultimate reticulations is glabrous. In the herbarium of the Arnold Arboretum the pistillate type was found under no. *21172*, *Madhuca elmeri* Merr., apparently some error having been made by Mr. Elmer in completing the labels, which makes me suspect that the same situation may exist elsewhere. The correct number is *21472*, for *21172* is the *Madhuca* and *21472* the *Laportea*.

LEGUMINOSAE

Crudia cauliflora sp. nov.

Arbor parva, foliis 1-foliolatis et ramulis glabris, fructibus caulinis, breviter denseque pubescentibus; ramis ramulisque teretibus, ultimis 1 mm. diametro; foliolis subcoriaceis, oblongo-ellipticis, 15–18 cm. longis, 6–7 cm. latis, basi late rotundatis, apice distincte sed obtuse acuminatis, siccis subtus brunneis, supra subolivaceis, subopacis; nervis primariis utrinque circiter 7, subtus paullo elevatis, laxis, patulis vel subpatulis, inter se 1.5–2.5 cm. distantibus, 1–1.5 cm. a margine arcuato-anastomosantibus, reticulis primariis laxis, ultimis subconfertis; petiolo cum petiolulo circiter 1 cm. longo; racemis caulinis, solitariis, vetustioribus glabris vel partibus ultimis breviter obscure pubescentibus, saltem 10 cm. longis (floribus ignotis); fructibus solitariis, compressis, oblongo-ellipticis, leviter inaequilateralibus, 8 cm. longis, 4 cm. latis, extus pallide brunneis et dense breviterque pubescentibus, seminibus 2 vel 3.

PHILIPPINE ISLANDS: Siargao: *Ramos & Pascasio*, Bur. Sci. *34921*, June 1919, the only known collection, TYPE in the herbarium of the Arnold Arboretum.

This was designated many years ago by me as new in the genus *Sindora*, but was never described, probably because I later realized that it could not represent any *Sindora*, and I had hoped that flowering specimens would eventually be received. It resembles several Malaysian species, such as *Crudia bantamensis* (Hassk.) Benth., *C. beccarii* Ridl., *C. curtisii* Prain, *C. reticulata* Merr., and even *C. subsimplicifolia* Merr. From all of these it is distinguished by its simple leaves being broadly rounded at the base; and from all described species of the genus it is distinguished by its solitary cauline racemes. None of De Wit's descriptions of the 18 Malayan species which he recognized in 1950 seems to apply to this species.*

Pithecellobium splendens (Miq.) Prain, Jour. As. Soc. Bengal 66(2): 516. 1897 (Novic. Ind. 350. 1905), ***Pithecolobium in nota.***

Albizzia splendens Miq. Fl. Ind. Bat. Suppl. 280. 1861.
Pithecolobium confertum Benth. Trans. Lin. Soc. **30:** 577. 1875; Bak. in Hook. f. Fl. Brit. Ind. **2:** 204. 1878; Prain in King, Jour. As. Soc. Bengal **66**(2): 264. 1897 [Mater. Fl. Malay. Penin. **3** (no. 9): 264], op. cit. 508; Ridl. Fl. Malay Penin. **1:** 661. 1922.

Malay Peninsula, Sumatra.

Prain's new binomial does not appear in Index Kewensis nor in any of its supplements to date, yet the publication of it is valid. From his own statement it is clear that he did not intend to replace Bentham's binomial by the one based on the earlier *Albizzia splendens* Miq., as he stated that it did not appear to him to be necessary or just, to rename Bentham's species because Miquel's description was based on leaf specimens only.

RUTACEAE

Glycosmis macrantha Merr. Univ. Calif. Publ. Bot. **15:** 114. 1929 (April 10).

Glycosmis oliveri Stapf ex Ridl. Kew Bull. **1930:** 80. 1930, **syn. nov.**

The types involved are *Beccari 2595* from Sarawak, for Stapf's species, and *Elmer 12134, 21456, 21528* from British North Borneo, on which the earlier published *G. macrantha* Merr. was based. The only reason for publishing this note is the fact that Tanaka has added annotations to some of the Elmer numbers accepting Stapf's specific name. It is unfortunate that Stapf did not publish his new species at the time he studied *Beccari 2595*, for in publishing its first description, Ridley's work was antedated nearly a year by the publication of *G. macrantha* Merr. The two species are identical.

* DE WIT, H. C. D. The genus Crudia Schreb. (Leguminosae) in the Malay Archipelago south of the Philippines. Bull. Jard. Bot. Buitenz. III. 18: 407–434. *fig. 1–3.* 1950.

MELIACEAE

Aglaia heterobotrys sp. nov. § Euaglaia.

Species *A. shawianae* Merr. affinis, differt foliis paullo minoribus, floribus breviter sed distincte pedicellatis, sepalis oblongis. Frutex vel arbor parva, foliis stricte 1-foliolatis, ramulis teretibus, pallidis, glabris, novellis circiter 2 mm. diametro, decidue breviter stellato-pubescentibus, indumento ferrugineo; foliis oblongo-ellipticis, chartaceis, 14–20 cm. longis, 4–7.5 cm. latis, basi late acutis vel subrotundatis, apice tenuiter acuminatis, acuminibus 1.5–2.5 cm. longis, obtusis, utrinque glabris, siccis pallide olivaceis, subnitidis; nervis primariis utrinque circiter 20, utrinque distinctis, elevatis, ad marginem arcuato-anastomosantibus; petiolo cum petiolulo 2–2.5 cm. longo, glabro; inflorescentiis in axillis superioribus, breviter stellato-pubescentibus, indumento ferrugineo, inferioribus simplicibus, ad 16 cm. longis, elongatis, floribus in partibus superioribus racemose dispositis, superioribus paniculatis, ad 14 cm. longis, pedunculatis, ramis primariis inferioribus 2.5 cm. longis, superioribus gradatim brevioribus, floribus racemose dispositis, pedicellis 0.5–1 mm. longis, bracteolis anguste lanceolatis, stellato-pubescentibus, ad 1 mm. longis; sepalis liberis vel subliberis, ad 1 mm. longis, oblongis vel anguste oblongis, obtusis vel subacutis, stellato-pubescentibus, 1 mm. longis; petalis 5, glabris, liberis, oblongo-obovatis vel late oblanceolatis, obtusis, 2 mm. longis, 0.6–1 mm. latis; tubo glabro, libero, 1.8 mm. longo, antheris 5, 0.4 mm. longis, inclusis, ovario dense pubescenti.

SUMATRA: East Coast, Kota Pinang District, Si Mandi Angin on the Soengei Kanan, topographic sheet 41, southeast corner, *Rahmat Si Toroes 4197*, April–May, 1933, with the local name *kajoe piran*.

The alliance of this species is clearly with that small group of simple-leaved species of which the Bornean *Aglaia triandra* Ridl., *A. odoardoi* Merr., *A. matthewsii* Merr., and *A. shawiana* Merr., as well as the Siamese *A. meliosmoides* Craib, are typical. It is distinguished by its vegetative and other characters, and particularly by its always racemosely arranged, shortly but distinctly pedicelled flowers. The inflorescences in the lower leaf axils are greatly elongated simple racemes, the flowers borne only along the upper 2 to 3 cm., but the uppermost inflorescence is a normal panicle.

Walsura monophylla Elm. Leafl. Philipp. Bot. 9: 3391. 1937, *descr. angl.*

Arbor 5.5 m. alta, inflorescentiis obscure pubescentibus exceptis glabra, foliis omnibus 1-foliolatis. Ramulis teretibus, glabris, lenticellatis, ultimis circiter 2 mm. diametro; foliolis oblongo-ellipticis, coriaceis, 11–28 cm. longis, 4–8 cm. latis, subtus pallidis, brevissime et acute acuminatis vel acutis, basi plerumque obtusis, nervis primariis utrinque 10–15, subpatulis, curvatis, arcuato-anastomosantibus, subtus distinctioribus; petiolo 1–2 cm.

longo; inflorescentiis terminalibus, anguste paniculatis, circiter 7 cm. longis, obscure pubescentibus, ramis primariis 1–1.5 cm. longis, patulis; floribus inter majores, flavido-albidis, circiter 4 mm. longis, 5-meris; sepalis triangulari-ovatis, acutis, obscure pubescentibus; petalis oblongis, obtusis vel subacutis, glabris, 4 mm. longis, 2 mm. latis; filamentis pubescentibus, tubo deorsum utrinque glabro; fructibus junioribus 5–8 mm. longis, breviter ellipsoideis vel subovoideis, pubescentibus.

A second Philippine collection of this species is *Ebalo 556* from Mount Langogan, near Puerto Princesa, Palawan, Feb. 23, 1940; the type is *Elmer 12903* from Brooks Point, Palawan. The above Latin description has been prepared to validate Elmer's binomial. The striking character of the species is its strictly 1-foliolate leaves, all other known species of the genus having pinnate leaves. It has long been known that *Aglaia*, another genus of the family, does contain a fair number of species with strictly simple leaves, although in the vast majority of its species the leaves are pinnate, and in all the known species of *Vavaea* the leaves are strictly simple. This reduction of pinnate leaves to simple ones in certain species of *Aglaia* is now paralleled in *Walsura*.

EUPHORBIACEAE

Aporosa cardiosperma (Gaertn.) comb. nov.

Croton cardiospermum Gaertn. Fruct. 2: 120. *pl. 107. fig.* [*11*]. 1791.
Agyneia latifolia Moon, Cat. Pl. Ceyl. 65. 1824.
Aporosa latifolia (Moon) Thwaites, Enum. Pl. Ceyl. 288. 1864; Trimen, Hand-book Fl. Ceyl. **4:** 39. 1898; Pax & Hoffm. Pflanzenr. **81** (IV. 147. XV): 96. 1922.

A species known only from Ceylon. The identity of Gaertner's species with that later described as *A. latifolia* (Moon) Thwaites was determined by Hallier f., Rec. Trav. Bot. Néerl. **15:** 35. 1918. According to Thwaites the native name *kebella*, cited by Gaertner, belongs with the distinctly different *Aporosa lindleyana* Baill., but the characters as described by Gaertner and the details of his figure are those of the Thwaites, not of the Baillon species.

At the end of volume two of his *De fructibus et seminibus plantarum*, Gaertner assembled under a center heading *Barbarae* nine alphabetically arranged taxa which he described and figured under their native names (Ceylon and Java), Fruct. 2: 485–488. *pl. 180.* 1791. Hallier f., op. cit., gave some attention to the identity of these, although the descriptions were manifestly not intended to represent new genera, nor are any binomials used. They are merely casual names for those fruits that Gaertner had which he could not refer to any described genus. A very few of these names have appeared in taxonomic literature as if genera were intended, and in two cases binomials are involved, although the latter were not originated by Gaertner. Hence, the identification of these old Gaertner taxa in terms of the binomial system is of only slight academic interest, as they scarcely bear on problems of nomenclature. The entries are as follows:

"*Balangue. E. madagasc.*"

This is the whole basis of *Balangue gaertneri* DC. Prodr. **8**: 316. 1844. It is possibly some rhamnaceous plant.

"*Cucumeroides.* Ex Japonia." = Trichosanthes.

"*Edokke zeylonens.*" = *Chaetocarpus castanocarpus* Thwaites.

"*Giek zeylonens.*" = *Odina wodier* Roxb. = *Lannea coromandelica* (Houtt.) Merrill, Jour. Arnold Arb. **19**: 353. 1938, *cum syn.*

"*Zoon zelonens.*" = *Schleichera oleosa* (Lour.) Oken, Allgem. Naturgesch. **3**(*2*): 1341. 1841; Merr. Interpret. Herb. Amb. 337. 1917, Jour. Arnold Arb. **31**: 284. 1950. (*Schleichera trijuga* Willd.).

This in earlier years, was referred to the menispermaceous *Pachygone ovata* (Poir.) Miers, and appears as a synonym of that species in the latest monographic treatment of the family, Diels, Pflanzenr. **46**(IV. 94): 343. 1910, where it does not belong. The binomial *K. zeylanicus* is currently credited to Gaertner, but he did not originate it. The earliest reference to it that I have located is in the synonymy of Miers' species, Hooker f. & Thomson in Hook. f., Fl. Ind. **1**: 105. 1872.

"*More zeylonens.*" = *Euphorbia longana* Lam.

"*Pite-heddija javan.*" = ?

"*Terme javan.*" = *Acronychia*?

"*Wal-tiedde* & *Keipisan Zeylonens.*" = ?

Apparently some menispermaceous plant, perhaps *Tiliacora*, is represented.

ANACARDIACEAE

Parishia maingayi Hook. f. Fl. Brit. Ind. **2**: 30. 1876; King, Jour. As. Soc. Bengal **65**(*2*): 493. 1896 (Mater. Fl. Malay. Penin. **2**: 779); Ridl. Fl. Malay Penin. **1**: 535. 1922.

Parishia elmeri Merr. Univ. Calif. Publ. Bot. **15**: 168. 1929, **syn. nov.**

I am now convinced that *Parishia elmeri* Merr. (1929), type from British North Borneo (Elmer *21662*) belongs with Hooker's species and it is accordingly reduced to the latter. This gives its range as the Malay Peninsula, Sumatra, Riouw, and Borneo, a very natural one. The Sumatran and Riouw specimens that I have seen are sterile.

Parishia malabog Merr. Philipp. Jour. Sci. **7**: Bot. 281. 1912, Enum. Philipp. Fl. Pl. **2**: 472. 1928.

Spondias romblonensis Elm. Leafl. Philipp. Bot. **10**: 3683. 1939, *descr. angl.*, **syn. nov.**

The type of Elmer's species, now reduced, is a staminate specimen, his number *12164* from Romblon. See the note at the end of my original description of 1912. Luzon (Tayabas), Mindoro, Ticao, Masbate, Sibuyan, Tablas, Romblon, Cebu, and Sibutu Islands. Endemic.

CELASTRACEAE

Celastrus paniculatus Willd. Sp. Pl. 1: 1125. 1798.

Alsodeia glabra Burgersdyk in Miquel, Pl. Jungh. 122. 1852; Miq. Fl. Ind. Bat. 1(2): 116. 1858; Oudem. Arch. Néerl. 2: 199. *pl. 9.* 1867, **syn. nov.**
Rinorea glabra O. Kuntze, Rev. Gen. Pl. 1: 42. 1891, **syn. nov.**

The type of *Alsodeia glabra* Burgersdyk, a fruiting specimen, was collected in Sumatra by Junghuhn. I had suspected from Oudeman's excellent illustration, because of the terminal panicle (in fruit) and other characters, that a *Celastrus* was represented and not a representative of the violaceous *Alsodeia* = *Rinorea*. Accordingly, while in Leiden I looked up the type and found that Hallier had already made the transfer to *Celastrus* in the herbarium but that he considered that a valid species of that genus was represented; I can find no record of his having published this conclusion. To me the Junghuhn specimen represents a form of the widely distributed *Celastrus paniculatus* Willd., type from India, the species, as currently interpreted, extending to Ceylon, Burma, Siam, Indo-China, southeastern China, the Philippines, Malay Peninsula (and now Sumatra), Java, and Timor. I have seen no specimens from Borneo, although it is to be expected there, as well as in Celebes and the Moluccas. Koorders, who in 1909 studied the type of *Flüggea ? serrata* Miq. (1858) from Java, correctly reduced that species to *Celastrus*, and further to *C. paniculatus* Willd. Other synonyms currently placed here are: *Celastrus alnifolius* D. Don, *C. dependens* Wall., *C. multiflorus* Roxb., *C. rothianus* Roem. & Schult., *C. metzianus* Turcz., *C. polybotrys* Turcz., *Ceanothus paniculatus* Roth., *Scutia paniculata* G. Don, and *Diosma serrata* Blanco.

Kurrimia robusta (Roxb.) Kurz, Jour. As. Soc. Bengal. 39(2): 73. 1870; Pitard in Lecomte, Fl. Gén. Indo-Chine 1: 893. 1912.

Celastrus robustus Roxb. Fl. Ind. 2: 395. 1824.
Bhesa moja Ham. ex Arn. Edinb. New Philos. Jour. 16: 315. 1834.
Rhesa moja Walp. Repert. 1: 538. 1842.
Kurrimia pulcherrima Wall. List no. 4334. 1830, *nom.*; Laws. in Hook. f. Fl. Brit. Ind. 1: 622. 1875, *descr.*
Nothocnestis sumatrana Miq. Fl. Ind. Bat. Suppl. 531. 1862.
Sarcosperma tonkinense H. Lecomte, Bull. Mus. Hist. Nat. Paris 24: 534. 1918, Fl. Gén. Indo-Chine 3: 914. 1930, **syn. nov.**

In their critical treatment of the Sarcaspermataceae, Lam and Varossieau, Blumea 3: 198. 1939, who had seen Lecomte's type, a fruiting specimen, correctly eliminated *Sarcosperma tonkinense* H. Lecomte from the genus and family and concluded that it was probably not even a sapotaceous plant; no identification of it was suggested. While in Paris in August 1950, I examined the type and at once the problem resolved itself. Manifestly Lecomte's type, *Bon 3974*, represents a species of the celastraceous *Kurrimia*, not a *Sarcosperma*. Direct comparisons then made showed that it was a fruiting specimen of the rather common and widely

distributed *Kurrimia robusta* (Roxb.) Kurz, which extends from Khasia and Silhet to Burma, Siam, and Indo-China southward to Singapore and Sumatra. I think that *Nothocnestis sumatrana* Miq. Fl. Ind. Bat. Suppl. 531. 1862, is correctly placed as a synonym of Roxburgh's species, for although I have not seen its type I take Netherl. Ind. For. Serv. *31688*, *32124* from Palembang, Sumatra, the type locality of Miquel's monotypic genus, to represent it, and I refer these two modern collections to *Kurrimia robusta* (Roxb.) Kurz.

RHAMNACEAE

Ventilago gamblei nom. nov.

Ventilago lanceolata Gamble, Kew Bull. **1916**: 134. 1916; Alston in Trimen Hand-book Fl. Ceyl. Suppl. 49. 1931, non Merr. (1915).

A new name is needed for this species of southern India and Ceylon, as the one selected by Gamble in 1916 had been used by me for a different Philippine species one year earlier.

ELAEOCARPACEAE

Elaeocarpus tectorius (Lour.) Poir. in Lam. Encycl. Suppl. *2*: 704. 1812, excl. fruct.; Merr. Trans. Am. Philos. Soc. II. **24**(2): 256. 1935.

Craspedum tectorium Lour. Fl. Cochinch. 336. 1790, ed. Willd. 411. 1793.
Dicera craspedum J. F. Gmel. ex DC. Prodr. **1**: 520. 1824.
Elaeocarpus robustus sensu Merr. Jour. Arnold Arb. **32**: 189. 1951, excl. syn. plur., non Roxb. § Chascanthus.

This is an endemic species of Indo-China erroneously placed as the equivalent of *Elaeocarpus robustus* Roxb., the type of which was from Silhet, India. In the rather extensive synonymy cited by me in 1951 only *Craspedum tectorium* Lour. and *Dicera craspedum* J. F. Gmel. actually belong with the Loureiro *Elaeocarpus* species above cited. Loureiro's genus and species were based on specimens from the vicinity of Hue, Indo-China. *Clemens 3688* (in flower) and *4156* (in fruit) were collected near Tourane, which is about 100 kilometers south of Hue. Clearly most of the Cochinchinese species characterized by Loureiro were observed in the vicinity of Hue, where he lived for many years. Both the Clemens' numbers are in the Paris and the University of California herbaria, and the first is also at Kew and the Arnold Arboretum. In 1951 I very critically compared the Kew specimen with the Loureiro one at the British Museum, and surely a single species is represented. *Clemens 3688* is with mature flowers; the Loureiro specimen has very immature buds.

The Loureiro original description is ample and well prepared. He unfortunately "guessed" at the fruit characters in his generic description of *Craspedum*, and for this reason Corner illogically refused to recognize *Craspedum tectorium* Lour. as worthy of consideration. I disagreed with

him then as I do now, for all one has to do is to exclude the description of the fruit in Loureiro's generic account of *Craspedum*; the specific description was wholly based on a flowering specimen.

Dr. Gagnepain in 1943 (Not. Syst. 11: 1–14) increased the number of Indo-Chinese species of *Elaeocarpus* by describing twelve new ones. He did not indicate the sections in accordance with Schlechter's scheme of classification, but no less than eight of them belong in *Chascanthus* by the indicated number of ovary cells (3) and the number of ovules in each cell (2).

This note is prepared to correct my error of 1951 when I misinterpreted Loureiro's species by reducing it to *Elaeocarpus robustus* Roxb. I add brief descriptive data based on the Loureiro specimen in the British Museum and *Clemens 3688, 4156* from near the type locality. Dr. Gagnepain left the two Clemens collections in the Paris herbarium without comment under the binomial *Elaeocarpus tectorius* (Lour.) Poir. which I assigned to them when the identifications were made by me and the sets of duplicates were distributed in 1927–28. I can only assume he approved of my identifications. I am indebted to Dr. Tardieu-Blot for checking the specimens.

Leaves nearly or quite glabrous, 7–13 cm. long and 3–5.5 cm. wide; lateral nerves 7 to 9 or 10 pairs; petiole 2–3.5 cm. long; flowers about 1 cm. in diameter, the petals 20–30-laciniate; ovary hairy, 3-celled, cells 2-ovulate. Fruit ellipsoid, sharply apiculate, practically glabrous, the bony endocarp very rugose. A photograph of the Loureiro specimens, a carbon rubbing of a full-grown leaf, and extensive notes are in the Arnold Arboretum herbarium; this was a second and later collection by Loureiro, sent by him as representing his species. The specimen is not the actual type.

DILLENIACEAE

Saurauia costata Reinw. ex de Vriese, Pl. Ind. Bat. Or. 56. 1856.

Saurauia warburgii Koord. Meded. Lands Plant. **19:** 354, 644. 1898, Suppl. Fl. Celeb. **2:** *pl. 80.* 1922 (poor), **3:** 39. 1922, **syn. nov.**

Reinwardt's species was based on material collected by him in October 1821 on Mount Sempo, Celebes, there being three sheets of this collection in the Rijksherbarium, Leiden. It is suspected that Koorders did not see these specimens, for otherwise he would scarcely have proposed *S. warburgii* Koord. as new in 1898. The latter was based on *Koorders 18954, 19283*, from Minahassa Province, northeastern Celebes. The several sheets representing the two supposedly different species are so similar that all might have been taken off the same plant or stand of plants.

De Vriese, in publishing Reinwardt's description, noted that this Celebes form resembled a Philippine collection, *Cuming 455*, which de described, l.c., as *Saurauia exasperata* De Vr.; this is, however, *Saurauia latibractea* Choisy (1854) as I understand that species, one that clearly is not closely allied to *S. costata* Reinw. Koorders stated that his new species was allied

to the Philippine *Saurauia elegans* (Choisy) F.-Vill. (*S. rugosa* Turcz.), and Stapf had noted on one of the Reinwardt sheets that it was "very near *S. rugosa* Turcz." In the latter species, which occurs in most provinces in Luzon and in Mindoro, the lax, long-peduncled, many-flowered inflorescences are up to 16 cm. long and 10 to 12 cm. wide, while its smaller leaves are, as Koorders noted, rounded, not cordate, at the base. He described the inflorescences of *E. warburgii* Koord. as only 2.5 cm. long. Although the vegetative characters of the two species are suggestively similar, I do not think that they are closely allied.

Saurauia lanceolata DC. Mém. Soc. Phys. Hist. Nat. Genève 1: 421. 1821, quoad descr., excl. *pl. 4*; DC. Prodr. 1: 526. 1824; De Vriese, Pl. Ind. Bat. Or. 39. 1856.

This is a very curious case. It is suspected that most authors have interpreted De Candolle's species from his distinctly good plate. His technical description was based wholly on a Javan specimen, *Leschenault 643*, the type being in the Paris herbarium. An excellent photograph of this type, kindly supplied by Madame Tardieu-Blot, is before me, including even the supplementary sheet with sketches of the flower and dissection notes. As will be seen from the photograph, the Leschenault specimen (*no. 643*) has only slightly developed inflorescences. This type should be compared critically with that of *Saurauia micrantha* Blume from Mt. Gede. Although no exact locality in Java is given for *S. lanceolata* DC., it would have to be from a readily accessible place, such as Mt. Gede.

The strange thing is how De Candolle's plate became associated with the Javan species. Zollinger, Syst. Verzeichn. 148. 1854, noted the great similarity of illustration to the South American *S. ruiziana* Steud., stating: "S. lanceolata DC. Mem. t. IV tam similis est S. Ruizianae Steud. (Ap[ateria] lanceolata D.C) ut nullomodo distincta videatur quamvis petalis basi coalitis. An de patria error quisdam in herbario Parisii adfuit?" Madame Tardieu-Blot says: "Le type est glabre (photo) et correspond à la description. Au contraire, la figure (Pl. IV) est très differente (velue) et cadre très bien avec S. Ruiziana." De Candolle's specific epithet has priority over any other designating a plant with which this type can be matched.

GUTTIFERAE

Calophyllum rotundifolium Ridl. Jour. Fed. Malay States Mus. 5: 22. 1914; Fl. Mal. Penin. 1: 188. 1922.

British North Borneo, Mount. Kinabalu, *Clemens 30984, 31428, 35038, 40705, 50316*. The altitudinal range is indicated on two labels as 4,000 and 5,000 ft. I cannot distinguish this strongly marked species from Ridley's type at Kew. The sessile, broadly cordate, suborbicular to broadly ovate leaves vary in length from 2 to 7 cm., their apices rounded or very broadly rounded occasionally slightly retuse. Malay Peninsula (Selangor), alt. 5000 ft. **New to Borneo.**

VIOLACEAE

Rinorea lanceolata (Roxb.) O. Kuntze, Rev. Gen. Pl. 1: 42. 1891.

Vareca lanceolata Roxb. Fl. Ind. 2: 446. 1824, ed. 2, 1: 648. 1832.
Celastrus pauciflora Wall. in Roxb. Fl. Ind. 2: 400. 1824.
Pentaloba lanceolata Wall. List no. 4023. 1830, *nom. nud.*
Pittosporum ? serrulatum Jack ex Griff. Calcutta Jour. Nat. Hist. 4: 195. 1843. **syn. nov.**
Alsodeia lanceolata Oudem. Arch. Néerl. 2: 196. *pl. 6.* 1867; Hook. f. Fl. Brit. Ind. 1: 188. 1872; King & Gamble, Jour. As. Soc. Bengal 58 (2): 404. 1889 (Mater. Fl. Malay. Penin. 1: 48); Ridl. Fl. Malay Penin. 1: 131. 1922.

For a rather sharply characterized species known only from Penang Island, this has accumulated a considerable synonymy. My attention was called to it through an attempt to place the generally ignored binomials *Pittosporum ? serrulatum* Jack and *Celastrus pauciflora* Wall., both based on Penang material. Jack sent a copy of his description to Wallich, who realized at once that no *Pittosporum* was represented, and, as he says he had no specimens from Jack, he apparently surmised from the description that *Celastrus* might be the proper place for it and so described it as his own species, although stating that the description was from Jack. Griffith, who edited the Calcutta reprint of Jack's plant descriptions in 1843, says that his data were from Jack's MS., yet these are the same as those published under *Celastrus pauciflora* Wall. It is suspected that Jack did send a specimen to Wallich which the latter failed to associate with Jack's manuscript description. Under *Vareca lanceolata* Roxb. Flora Ind. 2: 446. 1824, Wallich states: "I have specimens belonging probably to this plant, which were collected at Pinang by W. Jack, who in a Mss. note says: 'I am at a loss what to make of this shrub. I thought it might be a *Vareca* (according to Roxburgh) but the *capsule* is one-celled, *three-valved*, with parietal placentae.'" There is a specimen of *Wallich 4023*, type collection of *Pentaloba lanceolata* Wall. which, as far as the record goes, was not based on *Vareca lanceolata* Roxb., and two modern collections of the species from Penang in the herbarium of the Arnold Arboretum. As far as the two somewhat generalized descriptions of Jack and of Wallich are concerned, they agree in all respects with the characters of *Rinorea lanceolata* (Roxb.) O. Kuntze, the type of which was from Penang.

Rinorea semigyrata (Turcz.) J. J. Sm. in Koord. & Val. Meded. Dep. Landbouw 18: 73. 1914 (Bijdr. Boomsoort. Java 13: 73).

Pentaloba semigyrata Turcz. Bull. Soc. Nat. Moscou 27 (2): 342. 1854.
Alsodeia disticha Zoll. ex Teysm. & Binn. Cat. Hort. Bogor. 183. 1866, *nom.*, et in Miq. Ann. Mus. Bot. Lugd.-Bat. 4: 216. 1869, *nom.*, **syn. nov.**
Alsodeia semigyrata Turcz. ex Jacks. Ind. Kew. 1: 93. 1893.
Alsodeia paradoxa Blume ex Oudem. Arch. Néerl. 2: 204. *pl. 15.* 1867, et in Miq. Ann. Mus. Bot. Lugd.-Bat. 3: 71. 1867.
Rinorea paradoxa J. J. Sm. in Koord. & Val. op. cit. 67; Van Ooststr. in Backer Beknopte Fl. Java 4a (1): Fam. 48. 3. 1942.

Turczaninow's specific name is apparently the oldest valid one for this rare, or perhaps even extinct Javan species. His type was *Zollinger 2979*, and a duplicate of this collection is in the herbarium of the Arnold Arboretum, acquired in 1941 from the Boston Museum of Natural History, having originally been in the private herbarium of John Amory Lowell. The original description is short and unsatisfactory, leading J. J. Smith, who reproduced it in 1914, to think that perhaps some genus other than *Rinorea* was represented; yet he actually effected the transfer of the specific epithet to *Rinorea*. Van Ooststroom in 1942 apparently saw only the Blume material at Leiden, there being at least four sheets labeled by Blume as *Alsodeia paradoxa;* these specimens came from the Salak and Boerangrang Mountains, western Java. The region has been very intensively explored in the past century. He noted that the species had apparently not been collected since Blume's time. I cannot distinguish *Zollinger 2979* from these Blume specimens, its label merely indicating that it was collected in Java. It also bears an unpublished Zollinger binomial in *Imhofia*. This leads me to reduce, without question, the *nomen nudum*, *Alsodeia disticha* Zoll., as this specific epithet is the one that appears on our Zollinger specimen sub *Imhofia*. It is suspected that at first Zollinger thought that he had a representative of a new genus and then found that the generic name originally assigned to his number *2979* was a preoccupied one. Teijsmann and Binnendijk, who first printed the Zollinger binomial, merely indicate the species as being from "Ind. or." Some of the higher numbers of the Zollinger collection distributed under Java labels were actually from Sumatra.

I note that although *Rinorea semigyrata* J. J. Sm. was legitimately published in 1914, it was overlooked by the compilers to the supplements to Index Kewensis. Further I note that the binomial *Alsodeia semigyrata* was not actually published by Turczaninow, Bull. Soc. Nat. Mosc. 36(1): 559. 1863, as currently accepted. All that he stated was that his three species of *Pentaloba* (*P. corylifolia, P. fasciculata*, and *P. semigyrata*) represented species of *Alsodeia*, but he made no actual transfers.

LYTHRACEAE

Lagerstroemia speciosa (Linn.) Pers. (*L. flos-reginae* Retz.)

I have always been impressed by the apparent reluctance of certain taxonomists to accept changes in the accepted names of plants on the basis of the priority rule, no matter what the evidence is, and no matter what botanist upset the use of a generally accepted binomial strictly in accordance with the Code. A case in point is the very common and widely distributed *Lagerstroemia speciosa* (Linn.) Pers. versus the later *L. flos-reginae* Retz. When Koehne's monograph of the Lythraceae appeared (Pflanzenreich 17 (IV. 216): 1–326. *fig. 1–59*. 1903) he correctly accepted the Linnaean specific epithet, and as he was known to be a very critical worker, I did not hesitate to accept his conclusions. The species

extends from northern India southward and eastward through Malaysia to New Guinea and northeastern Australia, and is, I suppose, one of the most frequently collected of the arborescent species because it is so common and so conspicuous, when in flower, in most parts of its very wide range. From Koehne's references it is manifest that he had checked the first publication of the name-bringing binomial. I was therefore somewhat surprised to note that Mr. Corner, Gard. Bull. Straits Settl. 10; 272. 1939, rather curtly rejected *L. speciosa* (Linn.) Pers. and accepted the later *L. flos-reginae* Retz. He rested his case on King's statement, Jour. As. Soc. Bengal 67(2): 9. 1898, and manifestly did not check the original documents. King's whole argument is merely that the acceptance of the Linnaean specific name of 1771 was inadmissible, as "he describes *M[unchausia] speciosa* as a *shrub* [which is true, as Linnaeus does say "arbuscula"; he had a plant grown in a greenhouse in Germany], whereas this plant [*L. flos-reginae* Retz.] is a large tree; moreover the rest of the description would apply to various other species of *Lagerstroemia*." The last part of this statement is true, for the Linnaean description of 1771 is very short and very unsatisfactory. Yet the species is by no means always a large tree; I have seen immature plants in full flower on Luzon that were not more than 2 m. high. But what Koehne did not overlook, as did both King and Corner, is that the original description of *Munchausia speciosa* Linn. was published in Muenchhausen's Der Hausvater 5: 357. *pl. 2.* 1770. This description is not only an ample one, but it is accompanied by a really excellent plate; and the plant described and illustrated is in all respects *L. flos-reginae* Retz. = *L. speciosa* (L.) Pers. Yet Corner would maintain Retzius' specific name even at this late date. The description, according to Muenchhausen's own statement, was prepared by Linnaeus, in spite of the fact that a year later Linnaeus credited it to Muenchhausen. The specimens on which the description and the illustration were based were from a plant cultivated in the Botanical Garden at Goettingen, the source of it being stated as Java, and at the same time the common Javanese name *boengoes* was listed, the modern *boengoer* which is widely used in western Java. Muenchhausen said Java and China,—Linnaeus only China.

Turning to the Linnaean herbarium, a set of photographs of all the sheets being available at the Arnold Arboretum, there are three sheets in the *Munchausia* cover, none of them actually named by Linnaeus; but two of these are manifestly this very common *Lagerstroemia*, and for the most part the plate illustrating the species might have been drawn from these; and in Linnaeus' handwriting on one of these is the name *boengoes*.

We who attempt to apply the approved rules of nomenclature in the determination of the oldest valid specific name for this or that species are always subject to criticism on the part of those who apparently abhor changes in names of well-known species. Generally speaking it will probably be admitted that those who make changes try to do the best that they can with the data which are available to them. We all make mistakes, but that is no reason why we should be tacitly condemned merely because

we do, on occasion, correctly interpret a Linnaean type. There is no approved method whereby the oldest specific name can be abandoned in this case.

MYRSINACEAE

Ardisia oligocarpa nom. nov.

Ardisia oligantha Elm. Leafl. Philipp. Bot. 4: 1496. 1912; Merr. Enum. Philipp. Fl. Pl. 4: 260. 1923, non Baker (1885), nec Mez (1902).

The type and only known collection is *Elmer 12310* from Sibuyan, the flowers unknown. The species belongs in the subgenus *Pyrgus* in the alliance with *Ardisia perrottetiana* A. DC. and *A. serrata* Pers., but has much smaller, differently shaped, entire or nearly entire leaves, and short infructescences with very few fruits and apparently with very few flowers.

Ardisia diversifolia Koord. & Val. Meded. Lands Plant. 33: 249. 1900 (Bijdr. 5: 249).

Ardisia oligantha Mez, Pflanzenr. 9 (IV. 246): 134. 1902, **syn. nov.**
Ardisia javanica A. DC. var. *oligantha* Blume ex Scheff. Comm. Myrsin. Archipel. Ind. 74. 1867.

The Mez binomial was based on a single Reinwardt specimen from Mount Salatta, Java, in the Rijksherbarium, Leiden. It is not accounted for in Backer's recent treatment of the Myrsinaceae of Java, Beknopte Fl. Jav. VIIB Myrsinaceae 1–20. 1948. I do not see how this can be distinguished from the Koorders and Valeton species, of which Mez saw no specimens. He placed the latter next to his new one, stating "ex descriptione sequenti [*A. oligantha* Mez] peraffinis"; and in his key to the species on page 73 he apparently could discover no characters by which the two could be distinguished, merely inserting the Javan *A. diversifolia* Koord. & Val. between *A. verrucosa* Presl, a Philippine species, and *A. oligantha* Mez of Java, but indicating no separating characters

Ardisia taytayensis nom. nov.

Ardisia pachyphylla Merr. Philipp. Jour. Sci. 12: Bot. 157. 1917, Enum. Philipp. Fl. Pl. 3: 261. 1923, non Dunn (1912).

A species known from Palawan and Balabac, *Merrill 9188, 9216, Escritor* Bur. Sci. *21613*.

Discocalyx papuana (S. Moore) comb. nov.

Embelia papuana S. Moore, Trans. Linn. Soc. Bot. II. 9: 106. 1916.

The type and only known collection is a Boden-Kloss specimen, Wollaston expedition from Camp VIb Mt. Carstensz, New Guinea, alt. about 1200 m. This is clearly a small erect shrub, not scandent as are all representatives of *Embelia*; Moore did not indicate its habit, and there are no notes.

Embelia cotinoides (S. Moore) comb. nov.

Maesa cotinoides S. Moore, Trans. Linn. Soc. Bot. II. 9: 103. 1916.

The type of this in the herbarium of the British Museum is an excellent specimen collected by C. Boden-Kloss at Camp VIa Mt. Carstensz alt. 940 m. on the Wollaston expedition to New Guinea, 1912–13. It is in all respects an *Embelia* of the subgenus *Euembelia* in the general alliance with *Embelia sarasinorum* Mez of Celebes and the more widely distributed Malayan *E. coriacea* Wall. but is very distinct from both.

EMBELIA ? LUCIDA Wall. List no. 2315. 1830, *nom. nud.*, et ex A. DC. in Trans. Linn. Soc. 17: 134. 1834, *descr.*, Prodr. 8: 87. 1844 = **Antidesma coriaceum** Tul. Ann. Sci. Nat. Bot. III. 15: 204. 1851, non *Antidesma lucidum* Merr. (1906).

When a species is described as new but placed not only in the wrong genus but in a family remote from the one to which it belongs, it is sometimes worth while to prepare a record when a correct reduction can be made. Although Mez saw the holotype in the De Candolle herbarium, he was unable to place the species, merely indicating that it did not belong in the Myrsinaceae. At my request Mr. Burkill examined *Wallich 2315* at Kew, the type collection from Singapore, and reported to me that, although no flowers are left on the specimen (it was apparently pistillate, judging from De Candolle's description), *Embelia ? lucida* Wall. is safely the same as *Antidesma coriaceum* Tul. Other synonyms are *Antidesma fallax*, Muell.-Arg. (1865) and *A. pachyphyllum* Merr. (1916). Wallich's name cannot be used in *Antidesma* because of the different *Antidesma lucidum* Merr. (1906). Penang, Malay Peninsula, Singapore, Borneo; planted at Bogor, Java, fide Pax & Hoffmann.

Maesa megaphylla Merr. Philipp. Jour. Sci. 12: Bot. 158. 1917, Enum. Philipp. Fl. Pl. 3: 255. 1923.

Maesa lobuligera Mez, Repert. Sp. Nov. 16: 310. 1920.
Maesa megalobotrys Merr. op. cit. 20: 422. 1922, **syn. nov.**
Maesa celebica Koord. ex Koord.-Schum. Syst. Verzeich. Herb. Koord. 3: 100. 1914, *nom. nud.*, **syn. nov.**

The type of *Maesa megaphylla* Merr. was *Wenzel 1510* from Leyte, that of *M. lobuligera* Mez, *Foxworthy* Bur. Sci. *727* from Palawan, that of *M. megalobotrys* Merr., *Merrill 9176* from Palawan, and that of *M. celebica* Koord., *Koorders 18174* from Minahassa, northeastern Celebes. Had Koorders published a description of the latter, then his specific name would be the accepted one for this rather strongly marked species. The specimen of *Koorders 18174* at the Rijksherbarium, which I have seen, is fragmentary and sterile, consisting of a branchlet and two large glabrous detached leaves, these about 15 to 18 cm. long and 9 to 12 cm. wide. It is suspected that the reason why Koorders published no description is that he had only sterile material. In such a critical genus as *Maesa*, where

species are often distinguished by very slight characters, some might hesitate in reducing a binomial to synonymy where only vegetative parts are known, but the agreements in this case are so close, and the flora of northern Celebes is so similar to that of the Philippines, that I do not hesitate to place Koorders' name in synonymy. It is perhaps unreasonable to discuss the reduction of a mere *nomen nudum* in detail. Actual specimens now available to me are: Leyte, *Wenzel 1275, 1510, 1627* (two of these distributed under another binomial invalidated by *Maesa platyphylla* Elm.); Bohol, *Ramos* Bur. Sci. *43324*; Dinagat, *Ramos & Convocar* Bur. Sci. *84657*; Celebes, Minahassa, *Koorders 18174*. No specimen of *Merrill 9176* is at present available to me. From the description I had surmised that *Maesa megalobotrys* Merr. was not distinct from *M. megaphylla* Merr., and Dr. E. H. Walker, after examining an isotype of the former in the U. S. National Herbarium, confirms this reduction of it. It is also recorded from Palawan and from Mindanao.

OLEACEAE

Ligustrum robustum (Roxb.) Blume, Mus. Bot. Lugd.-Bat. 1: 313. 1850; Mansf. Bot. Jahrb. 59: Beibl. 132: 44. 1924, *cum syn.*

Phillyrea robusta Roxb. Fl. Ind. 1: 101. 1820.
Olea puberula Ridl. Jour. Straits Br. Roy. As. Soc. **59:** 128. 1911, Fl. Malay Penin. 2: 318. 1923, **syn. nov.**

In checking certain types of *Olea* at Kew in 1950 I noted a duplicate type of *Olea puberula* Ridl., i.e., *Ridley 15223* from Perlis, Malay Peninsula, and although the specimen is a poorly prepared one, manifestly *Ligustrum* rather than *Olea* is represented; this might be suspected from Ridley's description of his species as having terminal panicles. The note made at the time is to the effect that it was apparently a form of *Ligustrum robustum* (Roxb.) Blume with inflorescences narrower than in the typical form. As Roxburgh's species is currently interpreted, it extends from Nepaul, Silhet, Assam, and Bengal to Chittagong, Burma, Siam, Indo-China, and Sumatra, so that this extension of range to the Malay Peninsula is not surprising. For the present I prefer thus to dispose of Ridley's species, rather than by transferring his specific name to *Ligustrum*; in any case this is the first record of the genus *Ligustrum* for the Malay Peninsula.

Linociera pachyphylla sp. nov.

Arbor glabra, inflorescentiis parcissime pubescentibus exceptis, ramulis ultimis subpallidis, teretibus, consperse lenticellatis, 3–4 mm. diametro, nodis superioribus plus minusve compressis; foliis crasse coriaceis, rigidis, siccis utrinque brunneis vel castaneis, subconcoloribus vel subtus paullo pallidioribus, supra nitidis, oblongis vel oblongo-ellipticis, 18–27 cm. longis, 7–9 cm. latis, breviter subobtuse acuminatis, basi late acutis, nervis primariis utrinque 10–12, supra impressis, subtus elevatis, perspicuis, circiter ad marginem valde curvatis, fere anastomosantibus, reticulis pri-

mariis laxis, obscuris, secundariis obsoletis; petiolo crasso, 1.5–2 cm. longo; inflorescentiis axillaribus, solitariis, breviter pedunculatis vel e basi ramosis, 6–7 cm. longis, ramis primariis patulis vel adscendentibus; floribus numerosis, breviter pedicellatis, bracteis inferioribus crassissime coriaceis, ovatis, concavis, circiter 3 mm. longis, superioribus brevioribus; petalis fere liberis, loriformibus, obtusis, 5 mm. longis, basi circiter 1.5 mm. latis, sursum vix 1 mm. latis; antheris 1.1 mm. longis.

BORNEO: Sarawak: *Native collector 584*, notes lost.

This was distributed as representing *Linociera callophylla* (Blume) Knobl., but it proves to be remote from the species that Blume characterized. It belongs in the group with *Linociera pluriflora* Knobl., differing in its very rigid, thickly coriaceous leaves and shorter inflorescences. Other species in this assemblage are *L. nitens* Koord. and *L. verruculosa* Merr., but here again the vegetative characters alone separate this proposed new species.

Linociera stenura sp. nov.

Arbor glaberrima, ramulis ultimis gracilibus teretibus, 1 mm. diametro; foliis coriaceis, in sicco pallidis, vix vel obscure nitidis, utrinque subconcoloribus, lanceolatis vel oblongo-lanceolatis, basi acutis, 11–15 cm. longis, 2–4 cm. latis, ab infra medium sursum gradatim angustatis, apice longe graciliter caudato-acuminatis, acuminibus 1–2 cm. longis, obtusis; nervis primariis utrinque circiter 12, inter se plerumque 1–1.5 cm. distantibus, patulis, obscuris, 2–3 mm. a margine confluentibus, reticulis laxissimis, obscuris vel subobsoletis; petiolo 2.5 mm. longo; inflorescentiis axillaribus, solitariis, brevibus paucifloris, circiter 8 mm. longis, glabris; floribus usque ad 9, plerumque 3–5, breviter (1–1.5 mm.) pedicellatis, 4-meris, petalis linearibus, circiter 5 mm. longis, deorsum leviter ampliatis sed basi vix 0.5 mm. latis.

CELEBES: Malili District, *G. Kjellberg 2120*, August 19, 1929, a tree with white flowers on riverbank at Waraoe, altitude 50 m., TYPE in the Stockholm herbarium, a fragment in the herbarium of the Arnold Arboretum.

A species strikingly characterized by its distantly and obscurely nerved leaves which are very slenderly caudate-acuminate, gradually narrowed upward from below the middle, the obscure nerves spreading at nearly right angles and anastomosing with the equally inconspicuous and somewhat arched submarginal nerves 2–3 mm. from the leaf margin, the reticulations very lax, obscure or even subobsolete. Its few-flowered, axillary, solitary racemes are less than 1 cm. in length, even including the 5 mm. long very narrow petals.

Linociera ridleyi nom. nov.

Linociera cuspidate Ridl. Jour. Fed. Malay States Mus. 8 (4): 61. 1917, non Knobl. 1895.

The type of Ridley's species is a specimen collected on Korinchi Peak, Sumatra, at an altitude of about 7300 ft. He stated that it is allied to *Linociera montana* (Blume) DC. of Java.

Linociera sp.

Microtropis ? lanceolata Boerl. & Koord. in Koord.-Schum. Syst. Verzeich. Herb. Koord. **2:** 33. 1911.

The type of this species is *Koorders 10283* from Sumatra, a fruiting specimen which in 1940, on the basis of an actual examination of the type in the Bogor herbarium, we could not place other than as a species of *Linociera*, perhaps allied to *L. oligantha* Merr.; see Merrill & Freeman, "The Old World species of the celastraceous genus Microtropis Wallich," Proc. Am. Acad. Arts Sci. 73: 307. 1940. It seems as unwise now to propose a new name for this imperfectly known species in *Linociera* as it did to us in 1940. However, to call attention to this misplaced entity, it has been considered desirable to make a record of it in the family and genus to which the species manifestly belongs. *Linociera lanceolata* Knobl. (1933), the name of a Santo Domingo species, invalidates the use of the epithet of Boerlage and Koorders in *Linociera*.

APOCYNACEAE

Micrechites micrantha (Miq.) Hallier f. Jahrb. Hamb. Wissensch. Anstalt. 17: 156. 1899 (1900), *in nota*; Bakhuizen v. d. Brink in Backer, Beknopte Fl. Jav. 7B: Apoc. 32. 1948, Blumea **6:** 389. 1950.

Otopetalum micranthum Miq. Fl. Ind. Bat. **2:** 400. 1857, Versl. Meded. Kon. Akad. Wetensch. **6:** 191. 1857.
Ecdysanthera schrieckii Van Huerck & Muell.-Arg. Obs. Bot. 191. 1870.
Micrechites schrieckii Rolfe, Jour. Bot. **23:** 214. 1885; Vidal, Phan. Cuming. Philipp. 126. 1885; Merr. Enum. Philipp. Fl. Pl. **3:** 332. 1923.
Micrechites polyantha sensu King & Gamble, Jour. As. Soc. Bengal **74** (2): 504. 1907 [Mater. Fl. Malay. Penin. **4** (no. 19): 714], non Miquel.
Trachelospermum philippinense Elm. Leafl. Philipp. Bot. **2:** 488. 1908.
Micrechites furcata Ridl. Jour. Roy. As. Soc. Straits Br. **79:** 95. 1918, Fl. Malay Penin. **2:** 368. 1923.

This adjustment in the nomenclature of *Micrechites schrieckii* Rolfe, long considered to be a Philippine endemic, is necessary. Hallier f. in 1900, on the basis of a critical examination of its type specimen, determined the status of *Otopetalum micranthum* Miq. Miquel's description of its fruits as "Bacca corticata, semina intra pulpam fibrosum recepta (adhuc valde immatura)," and again in the species description as "baccae globosae ovoideae" is, of course, an impossible one for *Micrechites*, the fruits of which are slender follicles; what he actually mistook for immature fruits were corolla tubes deformed by insects. Boerlage, Handl. Fl. Nederl. Ind. 2: 379–380. 1899, had discussed this case previous to Hallier's extensive consideration of it. The latter actually utilized nearly six pages of print

in his greatly detailed study of the problem, and even then succeeded in burying his new binomial in the text (p. 156) as "*Micrechites micrantha* m." where all bibliographers overlooked it for nearly half a century (it still is not listed in Index Kewensis); and at the same time its name-bringing synonym is equally buried in the text on page 152. I suspect that even Bakhuizen van den Brink might have overlooked this strangely published new binomial but for the fact that Hallier had added a reference on the type sheet to "Kautsch. Lianen p. 156. 1900"; this I noted, in the herbarium, and this it was that led me to Bakhuizen van den Brink's 1948 consideration of the case. I accept the synonymy as given by him, and add several other binomials.

The species, as I now understand it, extends from Siam and the Malay Peninsula (*Maingay 1081*) to Sumatra, Java, and also occurs more or less throughout the Philippines. There are, however, available for study only comparatively few collections except for the Philippine area, where about twenty are available. Among the previously unlisted ones are *McGregor* Bur. Sci. *47371* from Tayabas Province, Luzon, *Ebalo 940* from Basilan, and *Wenzel 3403* from Surigao Province, Mindanao. There are in the Leiden herbarium certain Javan collections named by Blume as representing *Tabernaemontana polyantha* Blume which actually represent *Micrechites micrantha* (Miq.) Hall. f., but there are also other specimens which represent *Micrechites polyantha* (Blume) Miq. as currently understood. I follow Bakhuizen van den Brink in his interpretation of *M. micrantha* (Miq.) Hall. f.

VERBENACEAE

Clerodendron fortunei Hemsl. Jour. Linn. Soc. Bot. **26**: 259. 1890.

Clerodendron simile Merr. Govt. Lab. Publ. **35**: 64. 1906, non Pearson (1901), **syn. nov.**

Clerodendron mindorense Merr. Philipp. Jour. Sci. Bot. **7**: 342. 1912, Enum. Philipp. Fl. Pl. **3**: 404. 1923, **syn. nov.**

Hemsley's description of *Clerodendron fortunei* was based on two sheets of a *Fortune* collection merely indicated as coming from China. I had seen the type in 1935 and was then impressed with its close resemblance to certain Philippine forms. In September 1950 I again examined the type and compared it with specimens representing several Philippine species. I am now convinced that the *Fortune* specimens were taken from cultivated plants in China, for nothing like it has appeared in the very large collections made in southeastern and eastern China in the past thirty years. I do not hesitate to reduce the Philippine *C. simile* Merr. = *C. mindorense* Merr. to *C. fortunei* Hemsl. Hemsley described the corollas as 2 in. long; the longest one I observed was 4 cm. in length. Those of *C. mindorense* Merr. are 3 to 4 cm. long (original description 3 cm.). An allied form is *C. klemmei* Elm. from medium and higher altitudes in northern Luzon, but its corollas are 6 cm. in length.

Chinese associations with the Philippines have extended over a period

of about 2000 years. It is well known that they introduced into the Archipelago various economic plants, for a considerable number of these exotics are still known in the Philippines only by their Chinese names. Occasionally they also introduced an ornamental or merely curious species, as exemplified by Vidal's collection of the bignoniaceous *Markhamia caudafelina* (Hance) Craib in Albay Province, Luzon; see Sprague in Kew Bull. 1919: 310. 1919. The associations between Amoy and Manila were peculiarly close, and it may be that the Fortune collection came from plants cultivated at Amoy. On the other hand it is more than possible that they were taken from plants cultivated in the Fatee Gardens, across the river from Canton, which Fortune visited in 1843 and described the next year, Gard. Chron. 1844: 590. 1844. The Fatee Gardens still exist, being a series of nurseries on Lingnan Island where ornamental plants are propagated and sold. In the Philippines the species occurs at low altitudes, extending from northern Luzon to Mindoro, Semerara, Negros, and Mindanao. Additional collections at Kew are *Cuming 1475* from Batangas Province, Luzon, *Vidal 3453* from Laguna Province, Luzon, and *Loher 4414* from central Luzon. There is a photograph of Hemsley's type in the herbarium of the Arnold Arboretum.

Clerodendron cyrtophyllum Turcz. Bull. Soc. Nat. Moscou 36(1): 222. 1863.

Clerodendron amplius Hance, Ann. Sci. Nat. Bot. V. **5**: 233. 1866.
Clerodendron formosanum Maxim. Bull. Acad. Sci. St. Pétersb. **31**: 85. 1886, Mél. Biolog. **12**: 519. 1886.
Cordia venosa Hemsl. Jour. Linn. Soc. Bot. **26**: 143. 1890.

My interest in looking up Hemsley's type in 1950 was inspired by the same motives as was the case with *Clerodendron fortunei* Hemsl.; that is, that in the Boraginaceae nothing appeared in the very large modern collections from Chekiang that have passed through my hands in the past thirty years that even suggested the species Hemsley characterized. The actual type of *Cordia venosa* Hemsl. is a fruiting specimen from Ningpo. A casual examination of the type in August 1950 indicated what the difficulty was, for it represents the very common *Clerodendron cyrtophyllum* Turcz., Hemsley having erred in placing his fruiting specimen in the boraginaceous genus *Cordia*; as the type specimen was mounted one would conclude from a casual examination that its leaves were alternate; on the contrary they are opposite. Rehder had added to the sheet "cf. Clerodendron," and later, Jour. Arnold Arb. 12: 76. 1931, had actually reduced Hemsley's species to *Clerodendron cyrtophyllum* Turcz. This very common and characteristic species is now represented in the herbarium of the Arnold Arboretum by approximately a hundred individual collections, twenty-five of which are from Chekiang. Other areas represented are Anhwei, Hunan, Kiangsu, Kwangsi, Kweichow, Fukien, and Kwangtung provinces, Formosa, Hainan, and Indo-China. There is a photograph of Hemsley's type in the herbarium of the Arnold Arboretum.

RUBIACEAE

Canthium tavoyanum (Parker) comb. nov.

Plectronia tavoyana Parker, Kew Bull. **1925**: 429. 1925. Burma.

This change is made for the obvious reason that the generic name *Plectronia* Linnaeus has been misapplied by many modern botanists. The Linnaean type is a representative of the oliniaceous genus *Olinia* Thunberg. See Merrill, Philipp. Jour. Sci. **35**: 7. 1928.

Dentella serpyllifolia Wall. ms. "in sched. in Herb. Wall. sub 6206G." 1832, *nom. nud.*; Craib, Fl. Siam Enum. **2**: 27. 1932, *nom. subnud.*; Airy-Shaw, Kew Bull. **1932**: 289. 1932, *descr.*

LUZON: Rizal Province, *Bur. Sci. 1398*, August 1906, distributed as *Dentella repens* J. R. & G. Forster.

Curiously Wallich's accepted name does not appear in his lithographed List (generally cited as Catalogue), but Airy-Shaw apparently found it on a subsidiary label in the master set at Kew. The entry in the distributed lithographed List is under *Dentella repens* Forst., 6206"G? Ripa Irawaddi ad Henzada — 1826. (F[l]os distincta)." The species is now known to extend from Assam and northern Bengal to Burma, Siam, Lombok, Java, Mauritius, Luzon, and Guam (*Fosberg*). Curiously *Dentella repens* J. R. & G. Forst. has also been found in Guam, an intermediary stop, and at Acapulco, the terminus of the Manila-Acapulco galleon line (1565–1815). Both species are ruderals probably in part distributed by migratory birds, partly by man. This species is otherwise recorded from Polynesia only from the Marquesas Islands.

Ophiorrhiza sarawakensis nom. nov.

Ophiorrhiza reticulata Ridl. Sarawak Mus. Jour. **1** (2): 32. 1912, non Korth. (1851).

A new name is needed for the Bornean species characterized by Ridley in 1912.

Psychotria polytricha Miq. Fl. Ind. Bat. **2**: 287. 1857.

Psychotria rufipila Val. Ic. Bogor. **3**: 253, *pl. 291*. 1909, **syn. nov.**
Psychotria trichophlebia Merr. Mitt. Inst. Bot. Hamburg **7**: 295. 1937, **syn. nov.**

I now think but a single species is represented here. Miquel's species was based on *Korthals* specimens from Sumatra and Borneo; that of Valeton on Bornean specimens, *Teysmann 8000* and *Jaheri 509*; and that of myself on *Winkler 1571*, from Borneo. I have seen none of the cited specimens representing Valeton's species, but my concept of its limits is gained from his excellent illustration and ample description. *Beccari 822*, from Sumatra, in fruit, is currently referred to this species. There are

several old sheets at Leiden where the original records were lost or confused, labeled "Sumatra," "Moluccas" (this scratched), and "Java" (this very doubtful). I suspect that these were all from Sumatra or Borneo.

Psychotria sangeana (Miq.) comb. nov.

Chasalia sangeana Miq. Fl. Ind. Bat. Suppl. 546. 1862.
Psychotria rhodocarpa Teijsm. & Binn. Nat. Tijdschr. Nederl. Ind. 27: 30. 1864.

The type of Miquel's species was a *Teysmann* specimen from Sumatra. On the basis of the material in the Rijksherbarium representing two supposedly distinct species in different genera, both sent by Teysmann, I see no tangible differences and, although fruits are absent, I believe *Psychotria* to be its proper generic designation. Apparently at one time Valeton thought that *Uragoga* was represented, and later that the plant might be a small form of *Psychotria expansa* Blume. Miquel's older name is here adopted.

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SAURAUIA LANCEOLATA DC.
(TYPE, *Leschenault 643*)

STUDIES IN THE BORAGINACEAE, XXVII SOME GENERAL OBSERVATIONS CONCERNING THE LITHOSPERMEAE

IVAN M. JOHNSTON

IN THE PREVIOUS PAPERS of this series the genera composing the tribe Lithospermeae have been redescribed and individually discussed, Jour. Arnold Arb. 34: 258–299 (1953) and 35: 1–81 (1954). The tribe having been surveyed, we are now prepared to present a new key to the twenty-three genera concerned, and also some general observations concerning the tribe as a whole. Listed alphabetically the twenty-three genera of the Lithospermeae are as follows: *Alkanna*, *Ancistrocarya*, *Arnebia*, *Buglossoides*, *Cerinthe*, *Cystistemon* (includes *Vaupelia*), *Echioides*, *Echium*, *Halacsya*, **Lasiarrhenum*, *Lithodora*, *Lithospermum*, *Lobostemon*, **Macromeria*, *Maharanga*, *Moltkia*, **Nomosa*, *Onosma*, **Onosmodium*, **Perittostema*, *Podonosma*, **Psilolaemus*, and *Stenosolenium*. Six of the twenty-three genera are endemic to America (those marked with the asterisk), and sixteen are endemic to the Old World. Only one genus, *Lithospermum*, has species present in both the Old and the New World.

To be excluded from the Lithospermeae are a number of genera which at one time or another have been referred to it. These include *Moritzia*, *Thaumatocaryon*, *Antiphytum*, *Amblynotopsis*, *Amphibologyne*, *Sericostoma*, *Echiochilon*, *Megastoma*, *Myosotis*, *Mertensia*, *Trigonotis*, *Pulmonaria*, *Bothriospermum*, *Moltkiopsis*, *Mairetis* and *Neatostema*. Of these genera, *Pulmonaria* is best referred to the Anchuseae and *Bothriospermum* to the Cynoglosseae, and the remaining fourteen to the Eritricheae.

As to habit the Lithospermeae are prevailingly herbaceous perennials. Species having only an annual duration are relatively few and occur only in *Buglossoides*, *Arnebia*, *Stenosolenium*, *Cystistemon* (including *Vaupelia*), *Echium*, and *Cerinthe*. The cymes are abundantly bracted and usually conspicuously so in all members of the tribe except *Ancistrocarya*. Floral dimorphy in several forms is present in five genera within the tribe. Heterostyly in a very elaborate form is present in *Lithospermum*, *Echioides*, and *Arnebia*, and in a simple form in *Lithodora*. Elsewhere among the Boraginoideae heterostyly is reported only among species of *Anchusa* and *Pulmonaria* of the Anchuseae, among *Mertensia*, *Cryptantha*, and *Amsinckia* in the Eritrichieae, and in one species of *Paracaryum* in the Cynoglosseae. Gynodioecism is widespread within *Echium*. Outside the Lithospermeae it is known only in a few species of *Myosotis* and *Lindelofia*. Cleistogamy is developed in some species of *Lithospermum* and elsewhere in the subfamily is known only in *Neatostema*, *Cryptantha* and *Pectocarya*.

Deviations from radial symmetry in the flower are more common and widespread in the Lithospermeae than in any other group within the family. The corolla becomes distinctly zygomorphic in *Echium*, *Lobostemon*, *Halacsya*, *Alkanna*, and *Macromeria*. In addition, zygomorphy less evidently developed is also present in corollas of some species of *Cerinthe* and *Onosma*. Deviations from radial symmetry in the androecium occur in many Lithospermeae. Within the corolla the individual filaments may differ from one another in length, or in the form of their attachment, or in the height at which they are affixed to the corolla. Androecia deviating from radial symmetry occur in *Echium*, *Lobostemon*, *Alkanna*, *Moltkia*, *Lithodora*, *Maharanga*, *Cerinthe*, *Echioides*, *Arnebia*, *Stenosolenium*, and *Macromeria*. Outside the Lithospermeae decidedly zygomorphic corollas occur only in *Echiochilon* and *Lycopsis*. Differentiation among the members of the androecium, within the corolla, occur outside the Lithospermeae in *Echiochilon*, *Moltkiopsis*, *Lycopsis*, *Caccinia* (includes *Heliocarya*) and *Amsinckia*.

The frequency of yellow or orange as a corolla-color among the Lithospermeae is also noteworthy. Orange, yellow, or decidedly yellowish corollas occur in *Moltkia*, *Halacsya*, *Alkanna*, *Onosma*, *Podonosma*, *Cerinthe*, *Lithospermum*, *Echioides*, *Arnebia*, *Psilolaemus*, *Perittostema*, *Onosmodium*, and *Macromeria*. Within the tribe blue or bluish or pink corollas occur in *Echium*, *Lobostemon*, *Alkanna*, *Moltkia*, *Lithodora*, *Maharanga*, *Onosma*, *Cystistemon*, *Podonosma*, *Cerinthe*, *Arnebia*, *Stenosolenium*, *Buglossoides*, and *Ancistrocarya*. White corollas are normal in species of *Lithospermum*, *Buglossoides*, *Lasiarrhenum*, *Nomosa*, and *Onosmodium*. Blue, pinkish, or white corollas predominate in the other tribes of the Boraginoideae. Orange, yellow or yellowish corollas, however, are developed in other tribes by only a relatively few species of *Nonnea*, *Symphytum*, *Anchusa*, *Neatostema*, *Cryptantha*, *Hackelia*, *Amsinckia*, *Rindera*, *Lindelofia*, and *Cynoglossum*.

The corolla has an unappendaged throat in seventeen of the twenty-three genera of the Lithospermeae. Within the tribe there are only six genera in which intrusive faucal appendages are developed, viz. *Lithospermum*, *Buglossoides*, *Macromeria*, *Perittostema*, *Halacsya* and *Alkanna*. In the three other tribes of the Boraginoideae, however, the corolla is almost always provided with faucal appendages. Indeed, within the Anchuseae, Eritrichieae and Cynoglosseae there are only eight genera, out of more than sixty, in which the corolla is devoid of faucal appendages in all or nearly all of the species, i.e., *Moltkiopsis*, *Mairetis*, *Neatostema*, *Echiochilon*, *Sericostoma*, *Amphibologyne*, *Amsinckia* and *Trichodesma*. In the other genera in these three tribes the faucal appendages are well developed or are weak or absent only in a few species in which the corolla is much reduced in size, e.g., *Cryptantha*, *Plagiobothrys*, and *Pectocarya*.

The corollas of the Lithospermeae, unlike those in other tribes of the family, may bear stipitate glands on their inner surfaces, particularly so those in and directly below the corolla-throat. Stiped glands, sometimes in considerable abundance, are a feature inside the corollas of some or all

species of *Lithospermum*, *Macromeria*, *Lasiarrhenum*, *Perittostema*, *Arnebia*, *Buglossoides*, *Lithodora*, and *Alkanna*.

The corolla-throat in *Ancistrocarya* and in one species of *Lithodora* is densely strigose, a condition paralleled outside the tribes only in *Sericostoma* and *Echiochilon*. The corolla-tube (as distinguished from the corolla-throat) is hairy in species of *Lithospermum*, *Macromeria*, *Echioides*, and *Arnebia*. Outside of the Lithospermeae I know of a comparable condition only in the flowers of species of *Neatostema*, *Mertensia*, *Amsinckia*, and *Rochelia*.

The stamens in the Lithospermeae show a number of unusual features. In *Cerinthe*, *Podonosma*, *Cystistemon*, *Onosma*, and *Maharanga*, the anthers are connivent and become joined, in *Cerinthe* by the entangling of the caudate bases of the thecae, and in the other genera by lateral cohesion of the anthers. Outside of the Lithospermeae this condition is most closely approximated in *Borago* and *Trichodesma*. In these two genera the anthers are connivent, but in *Borago* they remain distinct, while in *Trichodesma* they become joined by the entangling of their contorted tips.

The anthers are terminated by an elongate sterile appendage in *Cerinthe*, *Podonosma*, *Onosma*, *Cystistemon*, *Maharanga*, and *Nomosa*. Outside of the present tribe only in *Trichodesma* of the Cynoglosseae does a comparable very elongate appendage terminate the anther. Small appendages terminate the anther in *Halacsya*, *Onosmodium*, *Lasiarrhenum*, and *Buglossoides*. Outside the tribe I know of such moderately appendaged anthers only in *Myosotis* and *Rochelia*.

In *Lasiarrhenum*, *Nomosa*, and one species of *Macromeria* the connective on the dorsum of the anther is hairy, and in *Halacsya* the margins of the thecae are densely short-ciliolate. These conditions appear to be unique in the family.

The filaments within the individual corolla are not whorled but affixed at different elevations above the corolla-base in species of *Lithodora*, *Alkanna*, *Echium*, *Lobostemon*, *Macromeria*, *Stenosolenium*, *Arnebia*, and *Echioides*. This unusual behavior is duplicated outside of the Lithospermeae only in *Echiochilon*, *Lycopsis*, and *Amsinckia*. The five filaments within the corolla are of different lengths in species of *Arnebia*, *Moltkia*, *Alkanna*, *Echium*, and *Lobostemon*. Outside of this tribe I know of this latter condition only in *Moltkiopsis*, *Echiochilon*, and *Caccinia*.

Although the pollen of the Boraginaceae, outside of the Lithospermeae, has not been systematically studied, there have been enough random examinations to indicate that the pollen of the Lithospermeae is notable for a high frequency of asymmetric types. Such pollen has the upper and lower halves of the grain differing in size and configuration. In lateral outline the grain may be ovate, conic-ovate, oblong-ovate, or be constricted above the pores and approach the outline of an hour-glass or a shoe-print. It is encircled by a row of pores, not about the equator, but below it, where the grain has its maximum diameter. Pollen of this sort is developed in *Alkanna*, *Echium*, *Lobostemon*, *Macromeria*, *Onosmodium*, *Nomosa*, *Lasiarrhenum*, *Ancistrocarya*, *Lithospermum*, *Podonosma*, *Cysti-*

stemon, and *Onosma*. At present this type of pollen is known only in genera of the Lithospermeae.

The style in the Lithospermeae may be short to elongate and be either included in the corolla or exserted from it. In *Arnebia* it may be simple, bilobed, forked, or bis-bifid. It is simply forked in *Echium* and *Stenosolenium* and frequently bilobed in *Lithodora* and *Alkanna*. The forked or bilobed style is not duplicated in other tribes of the Boraginoideae. Each lobe of the forked style is usually terminated by a stigma. When the style is simple it commonly bears two stigmas juxtaposed and terminal on its summit. In some genera, however, the two stigmas are separated and frequently over-topped by a bilobed sterile apex of the stylar column. In such cases the stigmas assume a subterminal position on the style and may become evidently lateral on it.

The subterminal stigmas are best developed in species of *Buglossoides* and *Lithospermum*. Unless the peculiar stigma of *Myosotis* proves to be similar, subterminal stigmas are well developed in other tribes of the Boraginoideae only in the genus *Sericostoma*. In most genera of the Lithospermeae the style is terminated by a pair of juxtaposed stigmas. Within the tribe the two stigmas usually remain distinct. In other tribes of the subfamily they are prevailingly united.

The nutlets of the Lithospermeae are prevailingly straight, erect, and basifixed, and in form are either ellipsoidal (and usually plump) or they are ovoid with the venter tending to be angulate and the apex coarsely beaked. Nutlets that are strongly compressed dorsi-ventrally, though frequent in the Eritrichieae and Cynoglosseae, are rare in the Lithospermeae and indeed are practically restricted to a few species of *Arnebia*. The ventral keel in various degrees may be obscure, broad and rounded, or narrow and prominent. There may be no evidence of a ventral suture or the suture may be marked only by a line that may be indistinct or sometimes interrupted. The suture is always tightly closed with its margins usually fused or firmly joined and never overlapping.

Several genera of the tribe have nutlets sufficiently unusual to be deserving of special comment. The 2-celled, 2-seeded nutlets of *Cerinthe* are well known. They apparently represent the congenital union of a pair of single-seeded nutlets. The condition is unique in the Boraginoideae. Also unique is the form of the nutlets of *Ancistrocarya*. From just above the broad base these gradually narrow into a very prolonged, slender, curved, sword-like beak which is hamate at the apex. The beak, which is nearly as long as the fertile portion of the nutlet, is a sterile prolongation of the pericarp-apex.

The bent nutlets of *Moltkia*, *Halacsya*, *Alkanna*, *Podonosma*, and some insular species of *Echium* represent another very unusual form of nutlet. Outside the tribe it is weakly represented only in *Neatostema* and some species of *Plagiobothrys*. In the Lithospermeae mentioned, the nutlets are basally affixed to the gynobase but only the lower half of the nutlet is erect. Above their middle they are bent 30–130° towards the ventral side. The seed within the nutlet is also bent. The cotyledons are vertical to

the attachment-end of the nutlet and the tip of the cotyledons is directly above the nutlet-attachment, the proper relation in a basifixed nutlet. In *Alkanna* and *Podonosma* the nutlet-body is so strongly curved that the attachment actually has the appearance of being lateral.

The nutlets of the Boraginoideae characteristically have a more or less convex dorsum and a usually angulate or medially carinate venter. An extreme departure from this conventional form is found in the nutlets of *Arnebia tetrastigma*. In that species, the sole member of *Arnebia* § *Euarnebia*, the nutlet has a plane or even slightly concave dorsum and a venter that is broadly convex with the ventral keel only very obscurely developed. The nutlets are also aberrant in having a cordate base and a T-shaped scar.

The nutlet of *Stenosolenium* bears its attachment-scar not sessile on the base of the nutlet-body but rather ventral to the proper base of the nutlet at the lower end of a downwardly directed hollow stipe originating high up on the ventral side of the nutlet. In all other genera of the Lithospermeae the attachment is on the base of the nutlet-body. It is small, short and substipitate in *Alkanna* and *Podonosma* but is relatively large, sessile, and commonly flabellate or ovate in other genera. The attachment is usually restricted to the base of the nutlet. In *Arnebia guttata* and *A. tetrastigma*, however, it has a noticeable prolongation upwards for a short distance above the base on the nutlet-venter. As a consequence it becomes somewhat T-shaped, especially in *A. tetrastigma*.

The attachment-scar is usually not only basal on the nutlet but also horizontal. When oblique it usually slopes upward only towards the ventral side of the nutlet-body and commonly only slightly so. A basal attachment-scar sloping upward, not towards the venter of the nutlet but rather towards the dorsum, is present only in *Buglossoides* § *Eubuglossoides* and perhaps in *Ancistrocarya*. The attachment of the nutlets in *Lithodora* is anomalous. The true base of the nutlet is permanently affixed to the gynobase, the nutlet being freed along a new plane of abscission developed a short distance above the morphological base of the nutlet.

The nutlets of the Lithospermeae may be smooth, verrucose, tumulose, or rugose, and the epidermis lustrous or opaque and smooth and shiny or minutely muriculate, verruculose, or papillate. The smooth, lustrous, pallid, porcelain-like nutlets characteristic of most species of *Lithospermum* occur elsewhere in the tribe only in *Macromeria*, *Onosmodium*, *Lasiarrhenum*, *Psilolaemus*, *Ancistrocarya*, and *Buglossoides* § *Margarospermum*. Roughened or at least opaque nutlets prevail in other genera of this group. In other tribes of the Boraginoideae the nutlets may be armed with numerous glochidiate subulate appendages, or the back of the nutlet may bear a coroniform or annulate appendage, or it may be encircled by an entire, toothed or lobed, spreading or upturned margin. Among the genera of the Lithospermeae, however, only a few species, in *Onosma*, *Echium*, and *Ancistrocarya*, have appendaged nutlets. Those of *Onosma tricerospermum* Lag., of Spain, bear three conspicuous spreading rigid subulate spines on the dorsum. The nutlets of all other species of *Onosma*

are unappendaged. In some of the Canary Island species of *Echium* (cf. Webb. & Berth., Phytogr. Canar. t. 146, 1844), the pericarp develops a few very exaggerated protuberances that give the nutlet the appearance of being coarsely lobed. The slenderly rostrate nutlets of *Ancistrocarya* have already been described. The nutlets of the Lithospermeae (like those of the Anchuseae) never bear glochidiate appendages nor epidorsal annulate or coroniform crests, nor is the back ever encircled by a differentiated margin.

My observations as to the orientation of the zygomorphic corollas in the Boraginoideae do not accord with the much quoted classical statements of the matter by Döll, Fl. Baden 2: 775–6, 778 (1859) and Eichler, Blüthendiagramme 1: 197 (1875). The calyx lobes of the boraginaceous flower are numbered by Eichler in the following order, 1, 3, 5, 2, and 4. Lobe no. 2 is identified as the one at the rear of the flower and as having a position opposite the rachis of the scorpioid cyme. This order appears to be correct, for in those flowers having very unequal calyx-lobes (e.g., *Cerinthe*) the largest outermost lobe, i.e., no. 1 according to Eichler, is always one of the two lobes on the abaxial or front side of the flower. With the calyx-lobes recognized as serviceable points of reference, it can be stated that according to Eichler the axis of the irregular corolla of *Echium* passes between the corolla-lobes alternating with calyx-lobe no. 4 and through the middle of the corolla-lobe alternating with calyx-lobes nos. 3 and 5. This gives the flowers of *Echium* a very strongly oblique plane of symmetry and places the 2-lobed lip of the corolla on the adaxial side of the flower.

In my study of herbarium material, I have found in *Echium*, *Lobostemon*, *Halacsya*, *Alkanna*, *Lycopsis*, and *Amsinckia*, that the axis in the bilaterally symmetrical corolla is oriented in such a manner that the 2-lobed lip of the corolla is abaxial and the 3-lobed lip adaxial. In these genera the plane of symmetry is only weakly oblique. It passes through the middle of the rear corolla-lobe (that alternating with calyx-lobes nos. 4 and 2) and between the corolla-lobes alternating with calyx-lobe no. 3. This is the same orientation that prevails in the zygomorphic corollas of the Solanaceae. It represents a deviation of only 36° from a truly medial orientation, not 72° as called for by Eichler.

Only in *Macromeria*, *Echiochilon*, and *Heliocarya* have I found in the Boraginaceae zygomorphic corollas with medial orientation, that is to say, so oriented that the rear (adaxial) lip was 2-lobed and the abaxial lip 3-lobed. In the flowers of these genera the axis apparently passes between the two rear corolla-lobes (those alternating with calyx-lobe no. 2) and also through the middle of the forward corolla-lobe, that alternating with calyx-lobes nos. 1 and 3. Medial orientation similar to this prevails in the corollas of the Verbenaceae and Labiatae. It represents an angular deviation of 36° from the axis of symmetry in *Echium*.

Enough evidence has accumulated from the study of herbarium specimens to cast considerable doubt on the accuracy of accounts in the books concerning the orientation of the bilaterally symmetric flowers of the Bora-

ginoideae. What is now needed is observations of flowers in the fresh state. The orientation should be determined not merely in the flowers having evidently zygomorphic corollas, but also in those in which the corolla may be only very obscurely bilateral or which depart from radial symmetry only in the androecium. Studies of symmetry are especially needed in *Lithodora*, *Moltkia*, *Stenosolenium*, *Arnebia*, *Echioides*, *Cerinthe*, *Onosma*, *Podonosma*, and *Moltkiopsis*. The orientation in the corolla of these genera needs to be determined not only in relation to the axis of the cyme, but also in relation to calyx-lobe no. 1, and particularly so when the latter is distinguishable by its size.

KEY TO THE GENERA OF THE LITHOSPERMEAE

Pollen bearing only 3 pores, grains in polar profile usually distinctly 3-sided.
Pollen-grains evidently colpate; thecae not ciliate; flowers not precociously sexual.
Nutlets strongly incurved, near the middle bent 90–130°, the attachment small and substipitate, appearing to be lateral but actually basal on the short erect lower section of the nutlet; herbage usually glanduliferous.
Corolla-lobes narrowly triangular, acute, soon reflexed; corolla-throat glabrous and devoid of faucal appendages and stipitate glands; anthers partially exserted. ..... **Podonosma.**
Corolla-lobes rounded, spreading; corolla-throat usually bearing stipitate glands; stamens and faucal appendages borne low in the corolla-throat and hence deeply included. ..... **Alkanna.**
Nutlets straight (or rarely bent in *Echium*); herbage not glanduliferous.
Anther lacking a prolonged sterile tip, remaining distinct; corolla usually evidently zygomorphic.
Annulus borne 1 mm. or less above the base of corolla-tube, composed of a minute collar or a ring of 5–10 minute sparingly hairy lobules; style almost always 2-lobed. ..... **Echium.**
Annulus developed 1.5–6 mm. above the corolla-base, represented by 5 evident densely villous swellings or 5 squamose appendages borne below the attachment of each stamen; style simple ..... **Lobostemon.**
Anther narrowed into a prolonged terminal appendage, commonly adnate at the base or along the sides to form a synandrium; corolla regular or practically so.
Corolla-lobes well developed, as long as or much longer than the corolla-tube, spreading or decurved; anthers coherent only along the margins of the terminal appendage, appendage evidently longer than the theca; filaments very short and usually bearing a thickened hairy basal appendage; tropical Arabia and Africa ..... **Cystistemon** and **Vaupelia.**
Corolla-lobes short, commonly about as long as broad, conspicuously much shorter than the tubular portion of the corolla; anthers usually coherent at the base and frequently also along the margin of the thecae and even along the margin of the terminal appendage, appendage usually shorter than the theca; filaments usually elongate, not appendaged at the base.
Calyx-lobes narrow, elongate, more or less parallel, separated by a

very narrow usually closed sinus; corolla without ribs projecting outward between the calyx-lobes; pollen ovoid to sphaeric or strongly oblate ..... **Onosma.**

Calyx-lobes more or less triangular, separated by an open triangular sinus; corolla with puffed-out ribs that project outward between the calyx-lobes; pollen cylindric or vertically ellipsoid. Himalaya and southwestern China ..... **Maharanga.**

Pollen-grains not at all colpate; anthers with thecae margined by a ciliate fringe of short stout crowded hairs; flowers precociously sexual, style and stamens exserted while the corolla is still incompletely developed; nutlets bent ..... **Halacsya.**

Pollen bearing 6 to many pores; grains circular or somewhat polygonal in polar profile.

Nutlets united in pairs, each nutlet 2-locular and 2-seeded; pollen evidently colpate; leaves cordate-amplexicaul at base ..... **Cerinthe.**

Nutlets not united, each one 1-celled and 1-seeded; pollen obscurely if at all colpate; leaves not cordate-amplexicaul.

Pollen-grains bearing 2 rows of pores, one at each end of the elongate grain.

Nutlet-attachment at the base of a downwardly directed stipe originating on the ventral side of the ascending nutlet-body ... **Stenosolenium.**

Nutlet-attachment on the base of the nutlet-body ..... **Arnebia.**

Pollen bearing only a single encircling row of pores.

Nutlets circumscissile above the base, their major seminiferous portion falling away leaving the short basal section persisting as a usually cupulate appendage permanently affixed to the gynobase .. **Lithodora.**

Nutlets detaching at the very base.

Throat of corolla glabrous and also devoid of stiped glands and faucal appendages.

Nutlets evidently bent at or near the middle; corolla blue or purple, or (in one species) yellow; filament evidently exserted from corolla-throat except in one species ..... **Moltkia.**

Nutlets straight.

Corolla salverform, the broad spreading yellow limb usually decorated with 5 evanescent black or purplish spots; stamens borne at unequal heights in the corolla-tube; Armenia, Caucasus and Azerbaijan ..... **Echioides.**

Corolla tubular, white or yellow, bearing no dark evanescent spots, lobes erect or ascending; stamens all arising at the same height in the corolla-throat; American.

Filaments about half the total length of the corolla, arising well below the middle of the corolla, base of filaments shaggy with slender multicellular gland-tipped hairs .... **Nomosa.**

Filaments about one tenth the length of the corolla or less, arising above the middle of the corolla, glabrous throughout.

Corolla-lobes narrow, acute or acuminate, very narrowly imbricate in the bud, sinus between lobes plicate, inflexed and thickened at base; pollen ovoid; leaves coarsely veined ..... **Onosmodium.**

Corolla-lobes ovate, broadly imbricate in the bud, sinus between lobes not plicate nor inflexed nor thickened at base; pollen ellipsoidal; leaves veinless or nearly so ..... **Psilolaemus.**

Throat of corolla decorated with appendages, stipitate glands or abundant hairs.
Nutlets gradually narrowed into a very prolonged beak, conspicuously rostrate with the tip hamate; cymes bractless above the very base; corolla-throat abundantly villose-strigose . . **Ancistrocarya.**
Nutlets not conspicuously rostrate, not hamate at the apex; cymes bracted throughout; corolla-throat not conspicuously hairy.
Filaments broadening upwards from the attachment, above the middle evidently broader than at the base.
Anthers conspicuously hairy on the back; filaments oblanceolate; corolla lacking faucal appendages; leaves broad and conspicuously veined . . . . . **Lasiarrhenum.**
Anthers glabrous, filaments deltoid to obovoid; corolla with faucal appendages; leaves very narrow, veinless . . . . . **Perittostema.**
Filaments linear or subulate or unguiculate.
Anthers completely exserted from the corolla-throat; corolla large, 39–90 mm. long, trumpet-shaped; filaments 6–70 mm. long . . . . . **Macromeria.**
Anthers completely included or only partially exserted from the corolla-throat; corolla usually less than 40 mm. long, salverform, funnelform or subtubular; filaments 0.5–5 mm. long.
Corolla-throat decorated inside with 5 well-developed vertical lines of hairs and stiped-glands . . . . . **Buglossoides.**
Corolla-throat lacking very well developed vertical lines of hairs and stiped glands, bearing localized faucal appendages or bearing scattered or localized congregations of stiped glands . . . . . **Lithospermum.**

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ECOTYPIC VARIATION OF THE PHOTOPERIODIC RESPONSE IN POPULUS

SCOTT S. PAULEY [1] AND THOMAS O. PERRY [2]

With eight text-figures

INTRODUCTION

DURING THE PAST FEW DECADES, the traditional and complacent notion that genetic differences within tree species are nonexistent or negligible has been gradually discarded. Most silviculturists are no longer content with the assumption that diversity within tree species can be adequately explained in terms of environment alone. Such a fundamental revision in biological theory has, quite naturally, produced a marked impact on silvical research methods and silvicultural practice.

The limitations, for example, of the descriptive method as a means of analyzing intraspecific diversity have become increasingly apparent. Although field observation and description of phenotypes and environment provide useful and essential preliminary data for the analysis of observed diversity, the method provides no means for determining the relative amounts of environmental fluctuation and genetic variation involved.

The solution of such silvical problems is, however, possible by transplant methods that have been perfected by various workers (Turesson, 19; Turrill, 20; Clausen, Keck and Heisey, 2; and others). One application involves the transplantation of different genetic types into a uniform environment. Under such conditions the effects of differences in habitat on the phenotype are eliminated, and the genotypes of different individuals of the group under investigation may be compared directly. For information on the rigidity or plasticity of genotypes, wild representatives of the species may be propagated vegetatively, and the clonal lines thus established may be planted under different environmental conditions. Both methods have been used in the photoperiodic studies here reported, and form one of the approaches to silvical problems currently under investigation by the Cabot Foundation.

Source of Material

Initial sampling of wild populations in *Populus* species native to North America was begun in the fall and winter of 1947–48, and has been continued annually since that time. During the period 1947–50 principal emphasis was placed on obtaining representatives of *P. trichocarpa* (western balsam poplar or so-called "northern black cottonwood"), native of the

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Pacific coast region, and the *P. deltoides* complex (eastern cottonwood) of the eastern United States. These collections were all in the form of branch or stem cuttings taken from what were determined to be average, healthy specimens growing under natural conditions at the various collection points. The use of cuttings was designed to insure that the clonal lines represented were derived from individuals known to be capable of survival in their native habitat. Since species in the section TACAMAHACA (balsam poplars) are uniformly good rooters from plants of any age, there was no need to restrict selected individuals of *P. trichocarpa* to the younger age classes. On the other hand, because of the poor rootability of cuttings from old trees, almost all of the *P. deltoides* clonal lines established were started from cuttings taken from plants 2 to 6 years of age.

The photoperiodic studies here reported are primarily concerned with clones of *P. trichocarpa* and the *P. deltoides* complex collected during the period 1947–50; but reference is also made to clonal line collections of *P. tacamahaca* (balsam poplar) made during the same period, and to collections of various other *Populus* species acquired in the spring of 1950 and subsequently.

Approximate ranges of *P. trichocarpa* and *P. deltoides* and the locality of origin for the various clonal lines of these species used in the photoperiodic studies are shown in FIGURE 1.

Although a portion of the field collection was done by the senior author, the bulk of the material was made available through the generous assistance and cooperation provided by numerous state and federal forestry agencies in the United States, and similar provincial and dominion organizations in Canada. Especially extensive contributions have been made by the U. S. Forest Service, U. S. Soil Conservation Service, Dominion Forest Service, and many state and provincial conservation departments within the ranges of the species concerned.

Experimental Areas

The principal propagation and test plantation site utilized by the Cabot Foundation is located in the town of Weston, Middlesex County, Massachusetts, about 10 miles west of Boston. The area is part of the former Case Estate, given to the Arnold Arboretum about a decade ago. The portion of several acres which has been allocated to the Cabot Foundation was formerly used as a pasture or mowing. The soil is, in general, uniform and the surface flat. The elevation is 200 feet, and lies somewhat lower than most of the surrounding area. For this reason temperature inversions in early fall may result in a somewhat shorter frost-free season than the average of 148 days for the Weston area as based on records of the Weston Weather Bureau Station (located ca. 2 miles northwest of the Case Estate at an elevation of 224 feet).

A portion of the Weston tract has been devoted to the propagation of the clonal lines assembled since the 1947–48 season, while the remainder of the area has been set aside for the establishment of permanent test plantations.

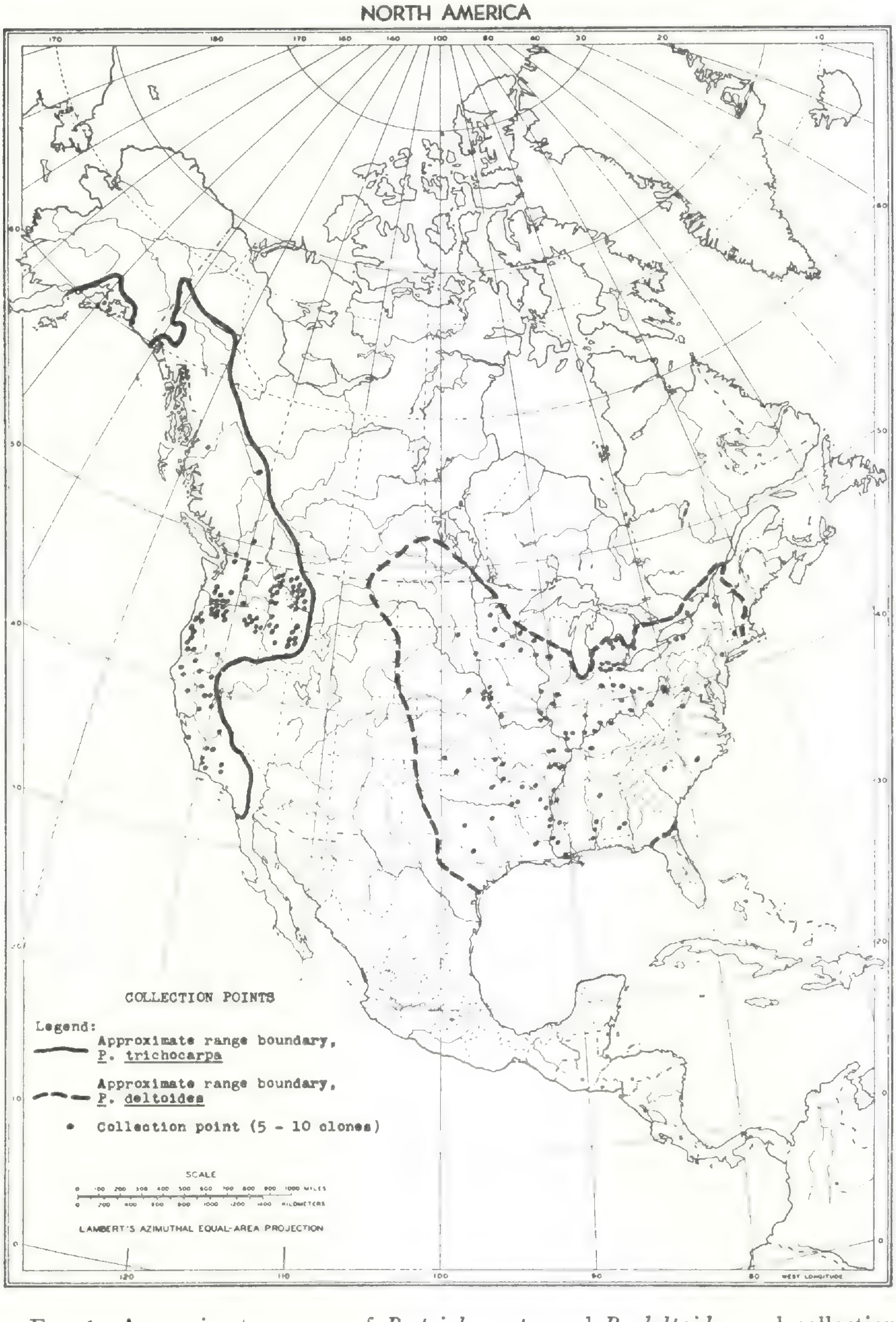

FIG. 1. Approximate ranges of *P. trichocarpa* and *P. deltoides* and collection points for clones used in this study.

Although two such plantations were established in 1950 and 1951, observations at Weston on the date of cessation of height growth for the various clones concerned in this study were all made in the propagation area, hereafter referred to simply as the "Weston area."

The combined experimental facilities of the Arnold Arboretum and the Bussey Institution, located in Jamaica Plain, Massachusetts, a part of greater Boston (ca. 10 miles southeast of Weston), have also been used in this study. The outdoor long-day and normal-day plots used in the 1951 experiments were set out in a portion of the experimental plots used jointly by these institutions, and located on a flat gravelly knoll in the first range of hills south of the Boston basin. The soil, thanks to continuous enrichment and good management, is highly fertile and uniform.

PHOTOPERIODIC RESPONSES IN PLANTS

Biologists, as well as most primitive peoples, have long recognized the indispensable nature of solar energy in the biological scheme. But only within the past thirty years have botanists recognized the notable significance to plant growth and development that is associated with the periodic manner in which this energy is supplied to the earth's surface.

Within the tropical and subtropical regions of the world, there is little change in the length of the daylight period throughout the year; but outside these regions, marked seasonal differences occur. At the latitude of Boston (ca. 42° N.), for example, the length of the daylight period on the shortest day of the year is ca. 9 hours, and on the longest day ca. 15 hours, i.e., a difference of 6 hours (FIG. 2). With increases in latitude the annual variation in day-length is greater. Thus, at the latitude of Juneau, Alaska (ca. 58° N.), day length at the time of the winter solstice is ca. 6.5 hours as compared with ca. 18.5 hours on the day of the summer solstice, a difference of 12 hours. The above day lengths are based on the time of sunrise and sunset. Actually, the effective photoperiods at all latitudes are somewhat greater due to the effects of the morning and evening twilight periods (Fig. 2).

Flowering Response

The response in growth and development exhibited by plants in relation to the length of the daily light period (i.e., *photoperiod*) is called *photoperiodism*. The earlier and, indeed, most of the later investigations concerned with this phenomenon have centered on the flowering response of various herbaceous plant species and varieties when exposed to photoperiods of varying length.

First recognition of the influence of day length on reproductive development in plants was made by Garner and Allard (3) in 1920. These workers observed that Maryland Mammoth tobacco, which normally does not flower in the field during the summer season at the latitude of Washington, D. C. did, nevertheless, flower profusely when grown in a green-

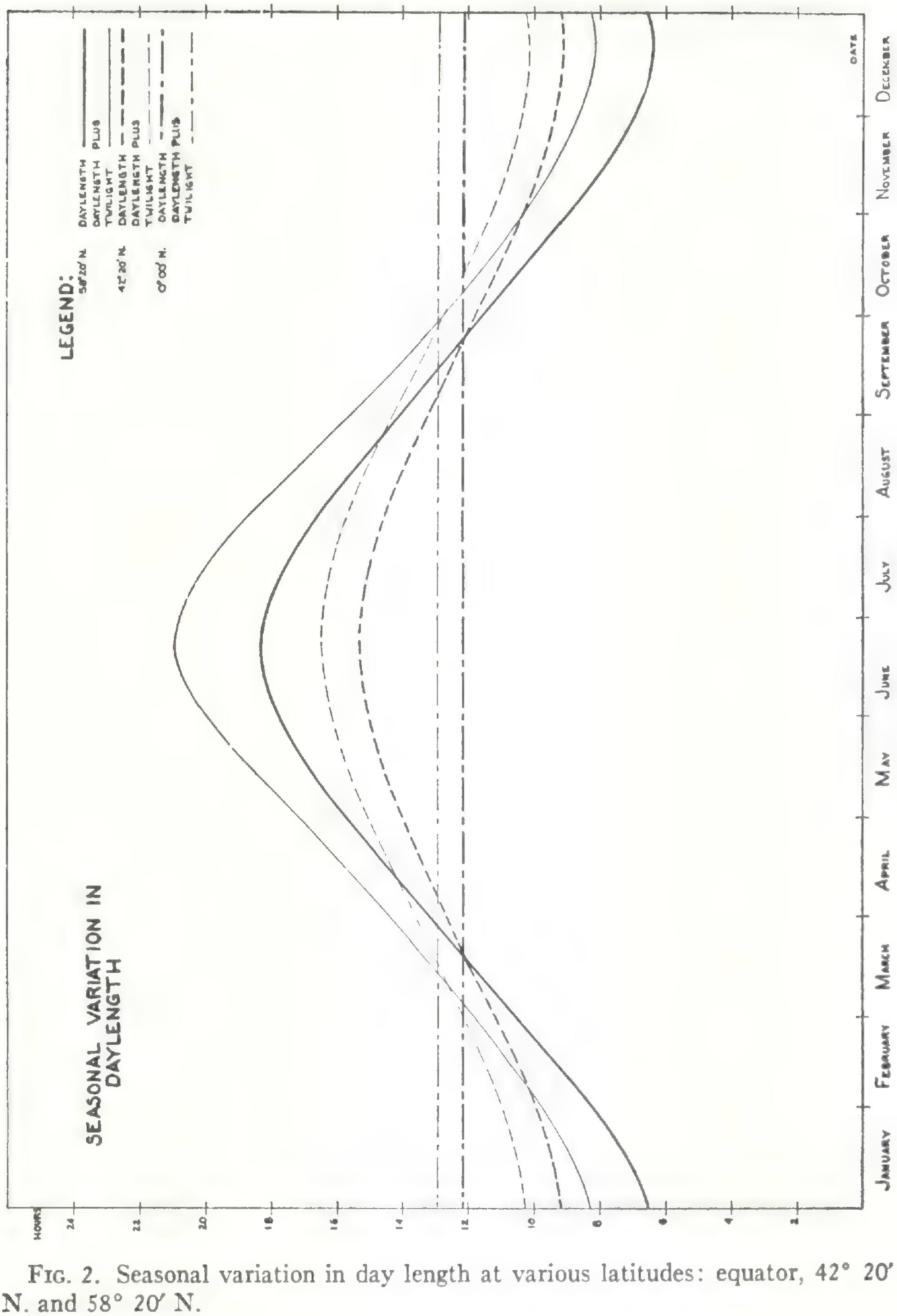

FIG. 2. Seasonal variation in day length at various latitudes: equator, 42° 20′ N. and 58° 20′ N.

house at the same latitude during the winter. The dissimilar reproductive development observed led to the hypothesis that day length was a controlling environmental factor, the relatively short photoperiods of winter apparently favoring flower production in this variety. Subsequent confirmation of this hypothesis was made through the use of carefully controlled experiments by these and numerous other workers.

The significance of the photoperiodic influence on flowering is obviously a matter of much practical concern in the case of cultivated crops grown for their fruit or seeds. Many of the grains, for example, require long days to flower, and for this reason long-day varieties cannot be successfully moved to southern latitudes. Other long-day plants grown for the food stored in their vegetative organs, such as spinach, lettuce, and radish, must be grown as spring or autumn crops in regions where the long days of summer would otherwise cause them to "bolt."

In order for such short-day plants as the Biloxi soy bean and numerous ornamentals (cosmos, aster, chrysanthemum, etc.) to flower, they must be grown either in the low latitudes or in the short days of spring or autumn in the higher latitudes. Many short-day ornamentals native of the tropics are, of course, grown successfully in greenhouses under the short-day regime of the winter months in northern latitudes.

Plants indeterminate with respect to their photoperiodic requirements for flowering, such as tomato, cotton, buckwheat, and sunflower, may be grown successfully over a wide range of latitudes.

Vegetative Response

Although major interest in the photoperiodic studies involving herbaceous plants has centered on the influence of day length upon reproductive development, most workers have also noted marked effects on vegetative growth as well. Most plants exhibit much better vegetative development when exposed to long photoperiods than to short ones, regardless of the fact that they may be classified as "short-" or "long-day" types with respect to flowering. Maryland Mammoth tobacco, for example, when grown under the long days of summer at the latitude of Washington, D. C., by Garner and Allard (3), attained heights of 10–15 feet; whereas, when greenhouse grown in the short days of winter, it did not exceed five feet.

Conversely, movement of long- or short-day flowering types into natural or artificially created shorter days usually results in marked reduction in vegetative development.

Photoperiodic studies of woody plants have for the most part involved seedlings, and consequently little is known of the influence of day length on reproductiveness. These investigations have, however, demonstrated that variation in day length is a factor of marked importance in the annual vegetative growth cycle of many woody species, particularly as it relates to the control exerted over the timing of physiological processes concerned in the onset of dormancy.

In common with techniques used in the investigation of photoperiodic

responses in herbs, studies of woody plants have involved the testing of various species in a day-length regime different from that prevailing in their native habitat. Whether such tests have involved actual movement of the plants north or south into a new natural day-length pattern, or if short or long days have been artificially created at any particular latitude, the results have been the same. In general, movement from the latitude of the natural habitat northward (i.e., into longer days) prolongs the active period of growth; and movement southward (i.e., into shorter days) shortens it. Such modifications in the length of the active growth period normally result in marked differences in total seasonal increment and frost hardiness. Thus, movement of plants into a day-length regime longer than that of the native habitat characteristically gives increased height growth accompanied by decreased resistance to early autumnal frosts; whereas movement into a short-day regime results in dwarfing, associated with increased frost resistance.

Similar photoperiodic growth responses have been, with but few exceptions, demonstrated by Moshkov (12, 13, 14) and Bogdanov (1) to characterize the behavior of various species in the following genera: *Acer*, *Aesculus*, *Ailanthus*, *Alnus*, *Caragana*, *Corylus*, *Fraxinus*, *Juglans*, *Larix*, *Phellodendron*, *Pinus*, *Prunus*, *Rhus*, *Robinia*, and *Ulmus*; by Kramer (8) and Jester and Kramer (6) in North American species of the following genera: *Acer*, *Fraxinus*, *Fagus*, *Robinia*, *Liriodendron*, *Liquidambar*, *Quercus*, and *Pinus*; by Sylvén (18) in the European aspen (*P. tremula*); by Johnsson (7) in *Betula*; by Langlet (9) in Scotch pine; and by Olmsted (15) in sugar maple.

INFLUENCE OF PHOTOPERIOD ON TIME OF HEIGHT GROWTH CESSATION IN *POPULUS*

First suggestions of photoperiodic sensitivity among the clones in the propagation area at Weston appeared during the first (1948) growing season. As a result of early height growth cessation and consequent dwarfing, *P. trichocarpa* ecotypes from high latitudes stood out in sharp contrast to those of more southerly origin.

Interclonal Responses to a Uniform Day Length

Precise measurements of height increment by the use of auxanometers of various design have been made by several workers. By their use the time of terminal growth cessation could doubtless be pinned down to a certain hour, or at least to a particular day. Such methods are not, however, practical for the measurement of large numbers of individuals in the field, since the cost would be prohibitive.

In the present studies total height measurements were taken to the nearest centimeter at 7-day, 5-day or 3-day intervals by direct measurement with meter sticks or tapes. Although lacking a high degree of precision, the technique is sufficiently accurate for determining comparative

differences in growth cessation which are spread over a period of several weeks or months. The error occurs during the period immediately preceding the time of actual height growth cessation. The increments between measurements during this period may be so small that the actual day of growth cessation is indeterminable. Depending upon the interval between measurements and other variables, deviations in the date of recorded growth cessation probably vary in the order of 3 to 7 days before and after the actual date of growth cessation. In general this method tends to encourage a later recording of growth cessation.

First systematic recording of the time of height growth cessation in the *Populus* collections was made during the 1950 season in the propagation area at Weston. Relatively small samples of *tacamahaca* and *deltoides* clones were included in the study, the majority being *trichocarpa*. All were derived from cuttings which had been planted in the spring of 1948 or 1949 and were thus in their second or third growing season. Measurements of total height for each of the clones included in the study were taken at weekly intervals from June 27 to November 7.

Active terminal growth in the group of *tacamahaca* clones measured was observed to occur over a period of about 158 days (April 14 to September 19); in the *deltoides* clones over a period of about 178 days (April 20 to October 15); and in the *trichocarpa* group over a period of about 197 days (April 14 to October 28). Although the first killing frost of autumn at Weston occurred the night of September 24–25, the growing season was by no means ended. Plants still in active height growth at that time (*deltoides* and *trichocarpa* of southern origin) suffered some damage to the young unfolding leaves near the growing point, but continued in active height growth thereafter. Subsequent light frosts in October (on the 6th, 8th, 16th, and 21st) caused similar damage; but height growth persisted in some clones until the first heavy frosts of October 26 and 27. These frosts were apparently of sufficient severity to kill all meristematic tissue in the growing points of the plants still active at that time.

The recorded dates of height growth cessation for the various *tacamahaca* clonal lines ranged from about June 20 [1] to September 19, a period of 91 days, representing 58 percent of the growing season. Among the *deltoides* group, cessation of height growth occurred between August 15 and October 18, a period of 64 days, or 31 percent of the growing season. The time of height growth cessation in the *trichocarpa* clones was considerably more widespread: first terminal growth cessation was recorded about June 20,[1] and the last on October 28, a period of 130 days, or about two-thirds of the growing season.

Since this considerable intraspecific diversity in time of terminal growth cessation occurred under the essentially uniform environment prevailing in the propagation area at Weston, the conclusion is inevitable that the vari-

[1] Measurements were started on June 27. This date proved too late to record the cessation of height growth of certain *tacamahaca* and *trichocarpa* clones of high latitude origin. Subsequent observations in 1951, 1952, and 1953 have confirmed that height growth in these clones stops ca. June 20.

ous clones within the species observed are genetically diverse in this character. That this diversity is not randomly distributed throughout the range of each species, but is inversely correlated with latitudinal distribution, is revealed by the scatter diagrams that result when latitude of origin for each clone of each species is plotted over the corresponding date on which height growth ceased at Weston (FIGS. 3, 4 and 5). The correlation coefficients for these diagrams are all high ($r = -.893$, $-.706$, and $-.823$ respectively), and all exceed the 1 percent level of significance.

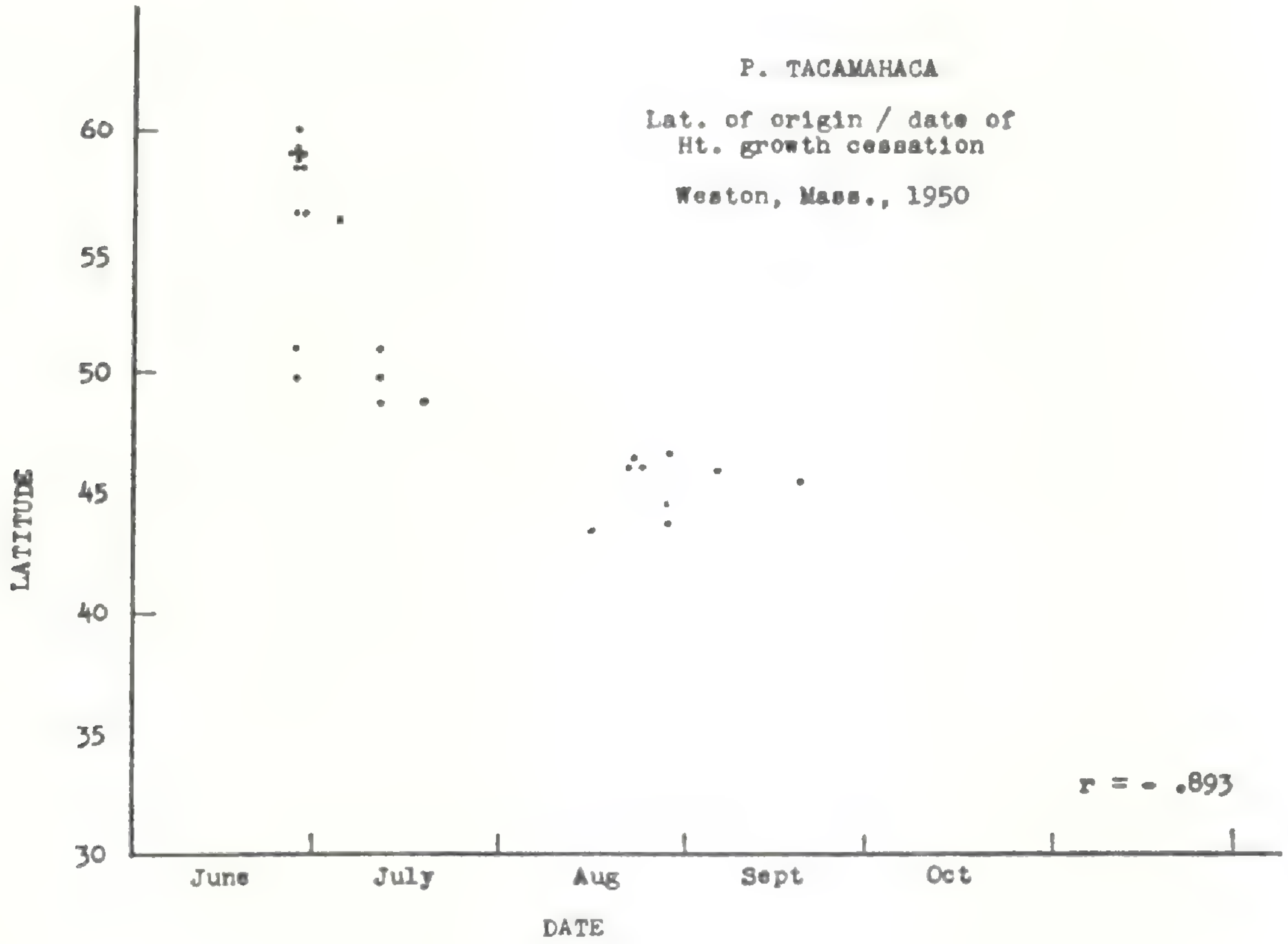

FIG. 3.

The trend of the gradient revealed by these diagrams clearly indicates a tendency for clones of high latitude (long-day) origin to cease terminal growth early, and clones of low latitude (short-day) origin to stop terminal growth late when grown under the mid-latitude day-length regime prevailing at Weston. These results are in agreement with the photoperiodic growth reactions which characterize the behavior of European aspen (Sylvén, 18) and species in other genera when subjected to day-length regimes differing from those in their native habitats. As previously pointed out, various workers have demonstrated that the movement of plants from native habitats of long day into short day is normally characterized by earlier height growth cessation; whereas movement from short day into long day results in delayed growth cessation. As a working hypothesis it therefore appears tenable to conclude that the inverse correlation between latitude of origin and time of terminal growth cessation for the ecotypes

of the *Populus* species here concerned is the result of similar photoperiodic reactions between the various genotypes of the ecotypes represented and the uniform day-length regime to which each was exposed at Weston.

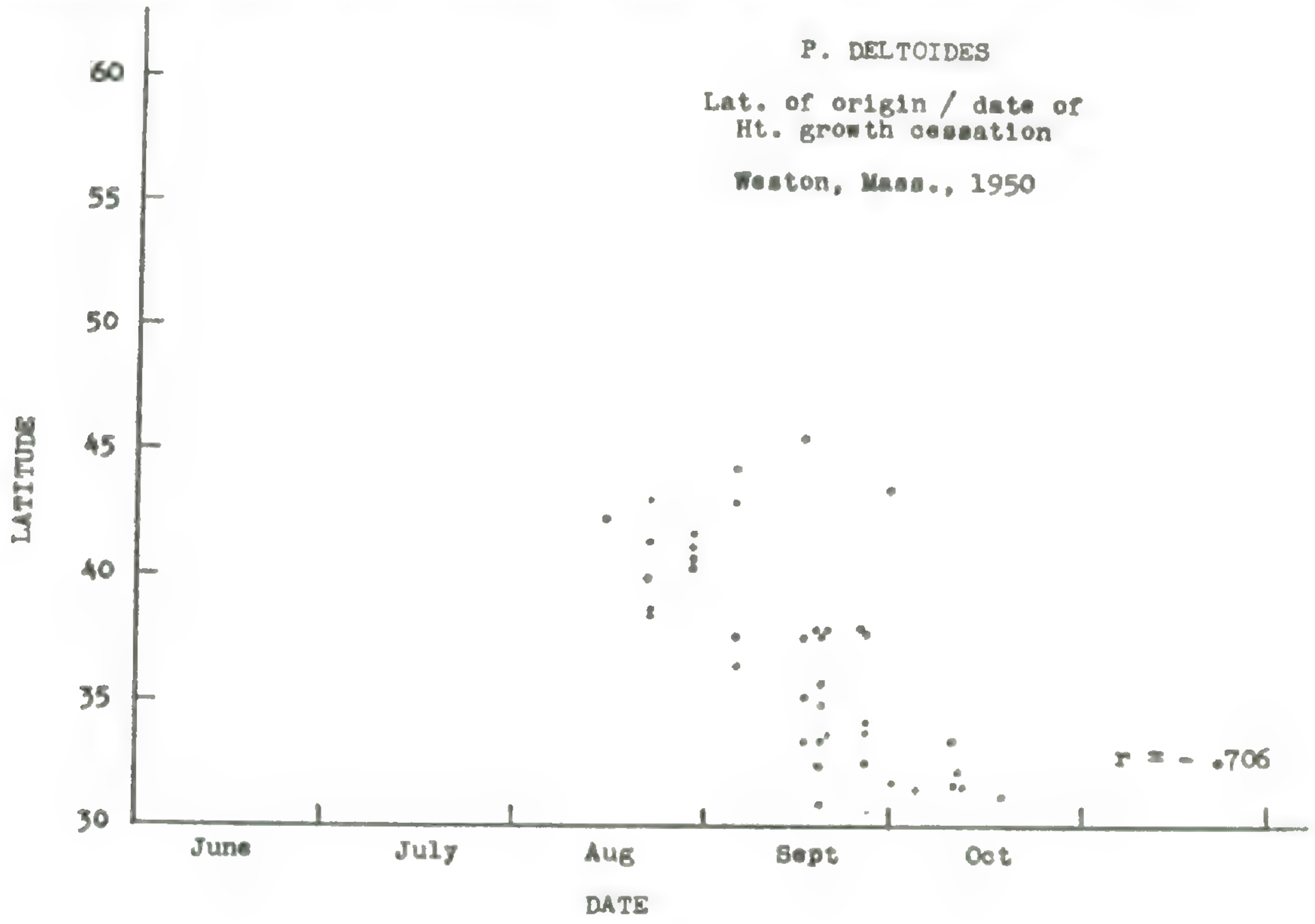

FIG. 4.

Although the clinal nature of the variation is sufficiently well-defined in these diagrams to support the above hypothesis, there is ample evidence to suggest that the relationship between time of height growth cessation at Weston and latitude of origin of the various clones is not necessarily simple and direct. The spread in dates of growth cessation from mid-July to late October among the *trichocarpa* clones native of latitudes between 40° and 50° (FIG. 5), for example, indicates that a pronounced local diversity in photoperiodic response exists, apparently quite independent of latitudinal origin.

That diversity in photoperiodic response may occur locally within a species population under essentially uniform day-length conditions leads to interesting speculation. There can be little doubt, in the first place, that height growth cessation in *Populus* signals the onset of initial physiological processes culminating in winter dormancy. The time during the growing season at which terminal growth cessation occurs thus assumes a role of critical survival value. Through the selective pressure exerted by the first killing frosts of autumn, only those genotypes capable of terminating height growth at a sufficiently early date to escape such frosts are capable of survival. Within any uniform day-length zone, therefore, where the growing season varies considerably in length, due to topography or other factors, the hypothesis may be made that adaptation to any particular

length of growing season is effected through the selection of those genotypes having a suitable photoperiodic response to the prevailing day-length regime of that latitude.

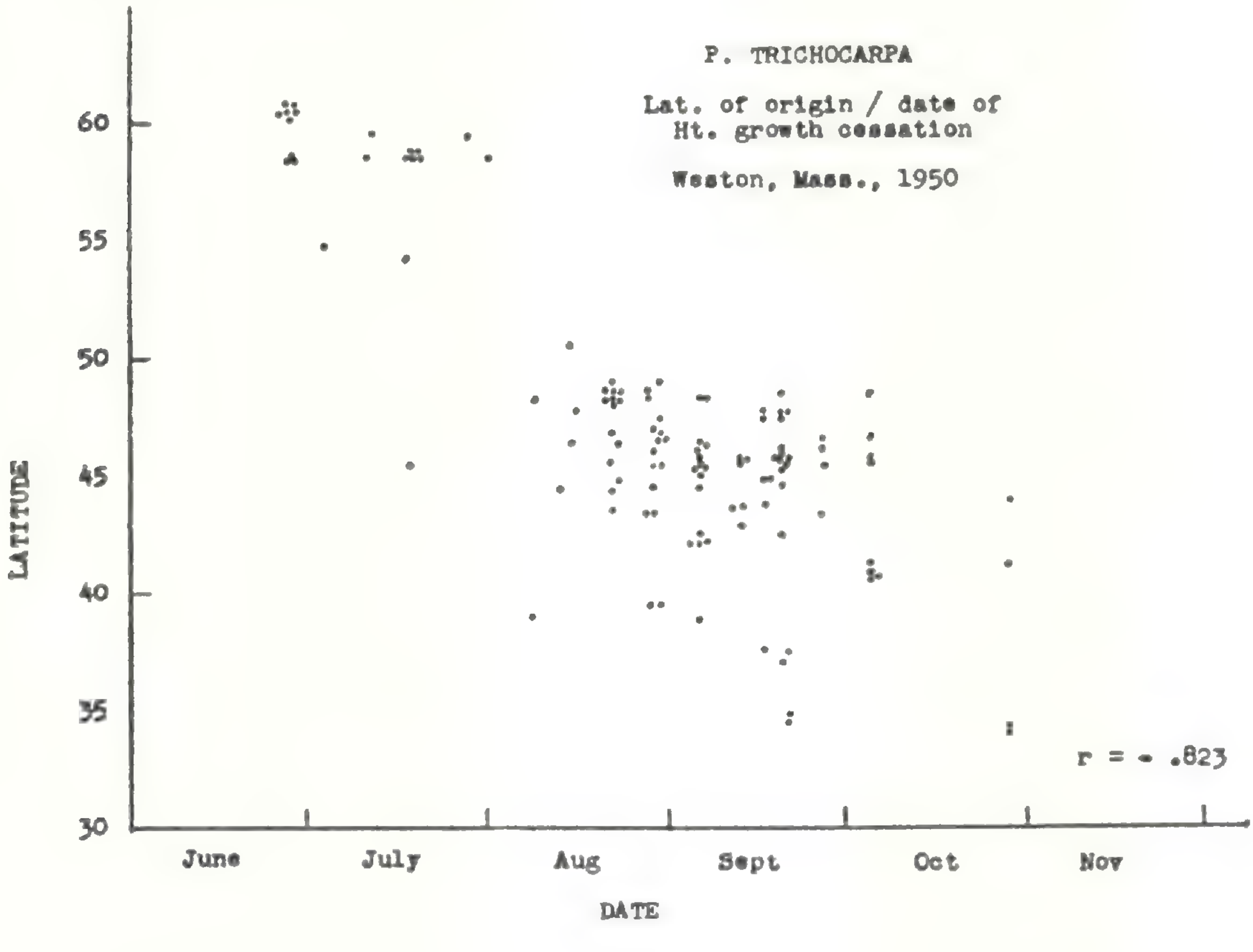

FIG. 5.

The group of clones originating between 40° and 50° (FIG. 5), referred to above, represents a case in point. This group is actually composed of a broad longitudinal sampling of *trichocarpa* ecotypes, extending from the Pacific coast to western Montana, and with a vertical dispersion from near sea level to ca. 5000 feet elevation. Since the length of the frost-free season in this latitudinal zone is, in fact, known to vary widely within comparatively short distances, due to elevation, the nature of the topography, etc., the considerable diversity in time of height growth cessation for clones native of the zone might be satisfactorily explained on the basis of the above hypothesis.

A direct test of the hypothesis may, of course, be made by determining the degree of correlation, if any, that may exist between the lengths of the growing season at the points of origin for clones native of a narrower latitudinal band (i.e., having an essentially uniform seasonal day-length regime) and the dates of height growth cessation for the same clones as recorded at Weston.

Although precise data on the average length of the growing season for the native habitats of each of the clones represented in our collections is for obvious reasons unavailable, reliable estimates nevertheless can be

made for those native to areas in the vicinity of U.S. Weather Bureau Stations (21).

FIGURE 6 shows the scatter diagram resulting when the length of the average growing season for those clones native only of the 2° latitudinal zone (45° to 47°) is plotted over the date of height growth cessation at Weston. The regression path here defined appears sufficiently uniform in trend ($r = +.789$ [1]) to confirm further the hypothesis that *trichocarpa* populations are capable of adaptation to growing seasons of varying length within uniform day-length zones by selection of those types having a suitable photoperiodic response.

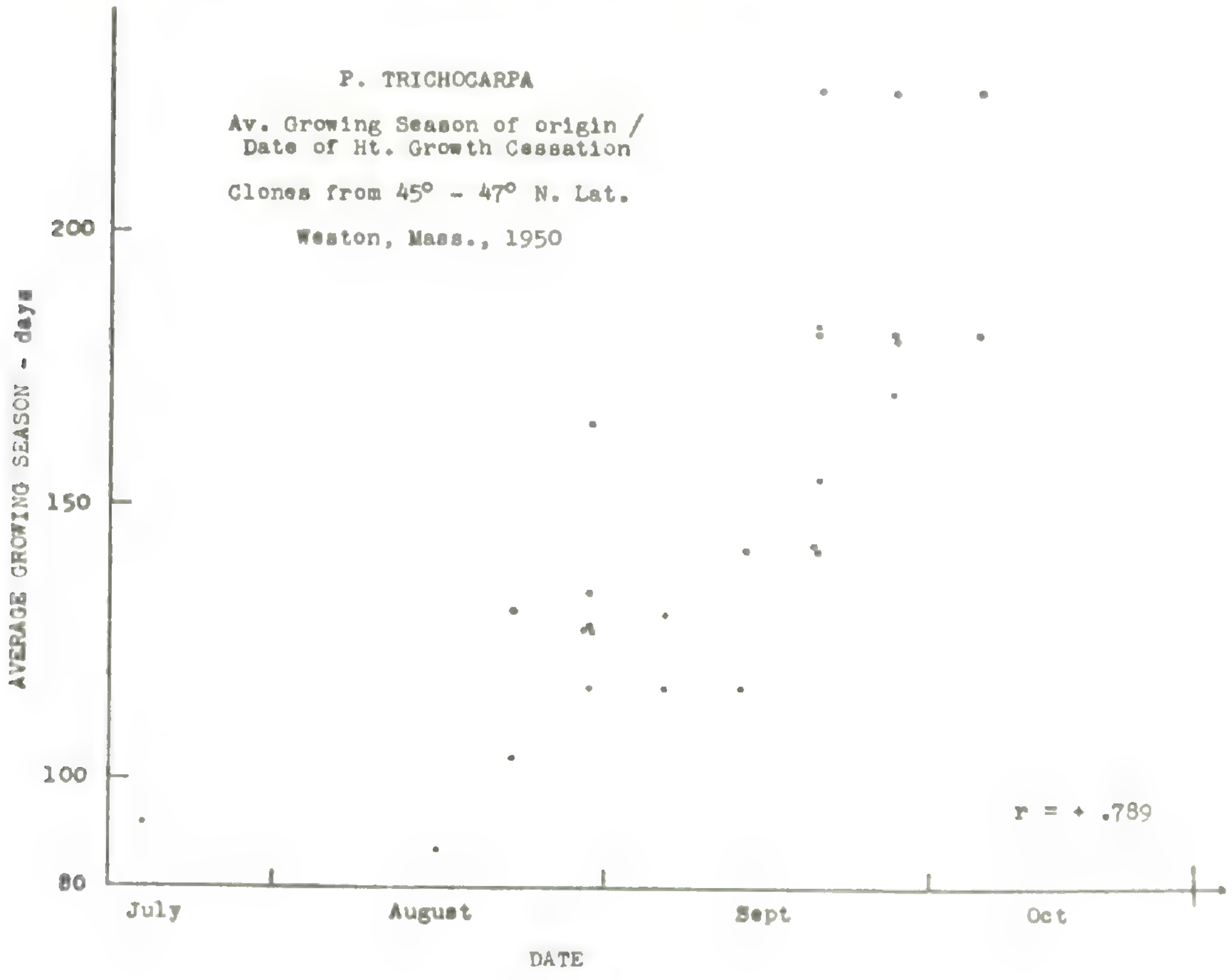

FIG. 6.

Intraclonal Responses to Diverse Day-length Patterns

During the 1950 and 1951 seasons, tests of photoperiodic sensitivity as revealed by influence on time of height growth cessation were made in about 100 clonal lines within the following species: *P. trichocarpa*, *P. tacamahaca*, *P. angustifolia*, *P. deltoides*, and various hybrids of *P. tremuloides* × *P. tremula*. The tests of 1950 were made in a greenhouse at the Arnold Arboretum with potted propagules of 45 clonal lines grown under short-, normal- and long-day photoperiods. Results of these observations have been previously published (Hoffmann, 4).

[1] Exceeds the 1 percent level of significance.

Similar tests of the same clonal lines, and about 55 additional, were made outside during the 1951 season in portions of the Bussey Institution nursery. Ramets of the various clones in these studies were exposed only to the natural-day pattern prevailing at the latitude of Boston (ca. 42° 20′ N.) and a long-day regime corresponding to that at Juneau, Alaska (ca. 58° 20′N.).

Flood lights and reflectors for the long-day plot were so arranged as to obtain complete coverage of the area with a minimum ground surface light intensity of 1.5 foot candles. Since the work of Withrow and Benedict (22), Matzke (10), and others demonstrates that light intensities of less than 1 foot candle are capable of producing photoperiodic responses, twice the duration of civil twilight was added to the "sunrise to sunset" day length (Fig. 2). According to Humphreys (5), light intensity at the beginning of civil twilight (morning sun 6° below the horizon) is 0.4 foot candle with a clear sky, and quickly rises above 1 foot candle.

Supplemental light was supplied the long-day plot by means of an automatic time switch in the morning and evening. Adjustment of the switch settings was made every third day to conform to the natural day at Juneau. Use of the lights was discontinued on September 30, when the photoperiod of Boston became greater than that of Juneau. Thereafter both experimental plots received the normal day length of Boston.

The variable responses in terms of height growth cessation to different day-length regimes that were observed added further confirmation of the presumed photoperiodic sensitivity in *Populus*, and also demonstrated the apparent similarity of this response to that exhibited by other tree genera of the temperate zone.

Detailed tabulation of the data recorded in these studies cannot, in the interest of brevity, be included in the present paper. However, a sample of the records on height growth cessation for *P. trichocarpa* clones of various origins when grown under the normal Boston-day and the artificial long-day regimes at the Arnold Arboretum during the 1951 season are shown in Table 1 (Columns 7 and 8). Differences in time of growth cessation are noted in Column 9. Included also are recorded dates of height growth cessation of the same clones under normal-day conditions at Weston in 1950 and 1951 (Columns 5 and 6).

As these data indicate, diversity of intra-clonal response to normal- and long-day regimes was most pronounced in those clones (981 and 984) from high latitude habitats. The net phenotypic disparity in height and leaf development between ramets of such northern clones when grown in the long-day regime to which they are adapted and the shorter-day regime of Boston is most striking (Fig. 7).

Similarly, marked intra-clonal differences in time of height growth cessation characterize those clones adapted to the high-elevation (short growing season) habitats in the lower latitudes when grown in the normal- and long-day regimes (clones 1047, 1485, and 1239, Table 1). In contrast, intraclonal diversity in response to normal- and long-day photoperiods demonstrated by those clones originating in the low-elevation (long grow-

ing season) habitats of the lower latitudes is characteristically small (clones 895, 899, 825, and 957, TABLE 1).

TABLE 1

TIME OF HEIGHT GROWTH CESSATION IN NORMAL- AND LONG-DAY REGIMES

P. trichocarpa

(1)	(2)	(3)	(4)	(5)	6)	(7)	(8)	(9)
	Origin			Date of Ht. Growth Cessation				
				Normal Day			Long Day	
				Weston		Arn. Arb.	Arn. Arb.	Difference (days)
Clone No.	Lat. (N)	Long. (W.)	Elev. (Ft.)	1950	1951	1951	1951	(8)–(7)
981	60–37	149–30	1300		6/25	6/20	8/28	69
984	60–19	149–21		....[1]	6/19	6/20	8/19	60
1147	48–30	115–55	1850	8/29	8/28	8/28	10/3	36
1151	48–25	114–30	2100	8/29	8/28	9/12	9/27	15
1565	48–10	114–10	8000	8/1	7/31	8/28	9/27	30
1029	47–30	123–55	250	9/19		9/21	10/5	14
1047	47–35	115–25	2400	9/12		8/29	9/28	30
895	46–10	122–55	30	9/26	9/18	10/3	10/12	9
1485	46–20	112–15	5000	8/15	8/7	8/10	9/13	34
899	45–35	122–35	25	9/26	9/18	10/7	10/12	5
1324	45–15	117–45	3400	9/5	8/28	9/18	10/3	15
825	44–30	123–25	200	9/19	9/18	10/5	10/11	6
1239	44–30	114–15	5200	8/29	8/28	8/31	10/3	33
957	43–25	123–25	500	9/26	9/18	10/6	10/11	5
1137	43–35	114–25	5300	8/29	8/28	8/31	9/27	27

[1] Height growth cessation occurred prior to June 27, 1950.

A point of considerable physiological interest is suggested by the results of the normal- and long-day tests. Theoretically, the net superiority in height shown by ramets of those clones grown in the long-day environment may be attributable to the combined influence of two causes: (1) the longer *season* of growth; and (2) the longer *daily* light period. Although the tests were not designed to analyze quantitative growth differences, the available data suggest that the longer daily light period did not materially contribute to the net seasonal height increment of plants grown in the long day. The superiority in the height of plants given the long-day treatment appears, thus, to have resulted solely from their longer growing season.

Other Environmental Factors Influencing Time of Height Growth Cessation

In general, little disparity was noted in the time of height growth cessation among ramets of the various clones when grown under the influence of the same day-length regime during the same or even succeeding seasons

(TABLE 1). Most minor fluctuations (1 to 10 days) may doubtless be attributed to inaccuracies inherent in the measurement technique employed. Others, demonstrating fluctuations of a higher order, such as the 21-day difference in date of height growth cessation of clone 1324 (TABLE 1) as recorded at Weston and the Arnold Arboretum in 1951, suggest the modifying influence of other factors on the photoperiodic reaction.

FIG. 7. Diversity in phenotype demonstrated by ramets of *P. trichocarpa* clone No. 984 when grown in the normal day-length regime of Boston (*left*); and in an artificially created long-day regime approximating that of its native Alaskan habitat (*right*). Height growth ceased in the ramet exposed to Boston day length on June 20, 1951; that exposed to the long-day regime stopped growth 60 days later (August 19, 1951). Scale is in feet.

That other environmental factors should serve to modify the photoperiodic response is by no means unusual. Among the factors most suspect is temperature. Garner and Allard (3) observed modification in the photoperiodic requirement for soy beans when grown in different temperatures, and similar reports have been made by other workers (Roberts and Struckmeyer, 17; and Parker and Borthwick, 16). Since most differences in time of height growth cessation between ramets of the same clone

grown at Weston and the Arnold Arboretum were due to earlier cessation of growth at Weston, the uniformly lower temperatures of that locality may have been responsible. (Differences in the natural day length of the two localities is negligible, since they are separated by only ca. 2 minutes of latitude.)

On the basis of experiments currently in progress, there is evidence that ramets of a clone grown in sod may be induced to stop height growth at an earlier date than those grown in cleanly cultivated soil.

There is some indication that excesses of available nitrogen in the soil (Kramer, 8) delay the onset of dormancy in apple trees, and this factor may thus influence time of height growth cessation.

In addition to the above factors, the quite empirical conclusion may be drawn that an apparent intraclonal diversity in physiological functions may frequently develop among ramets of a clone. Such differences appear to be associated with mechanical injury or attack by disease or insects.

ROLE OF THE PHOTOPERIODIC RESPONSE IN THE ANNUAL GROWTH CYCLE OF *POPULUS* SPECIES

Break of Dormancy and Early Seasonal Growth

Although light exerts a profound influence on growth activity during a large portion of the growing season in *Populus*, neither light nor its periodicity appears to be directly concerned in the break of dormancy.

In the propagation area at Weston, marked intra- and interspecific differences in time of leaf flushing are annually observable in early spring; but preliminary results of forcing studies made in 1950, 1951, and 1952 indicated that such differences reflect a diversity in response to prevailing temperatures, apparently acting quite independently of the light environment. In order to test more adequately for a possible light influence on dormancy break, ramets of various clones and sibs of several progenies representing species in all sections of *Populus* were grown in continuous light, natural day, and continuous darkness for a period of ca. three months in the late winter and early spring of 1953. The three compartments were maintained at as uniform a temperature as the facilities available permitted (ca. 70° F.).

Significantly, break of dormancy was negotiated without apparent incident by all plants in the dark compartment.[1] Within those clones and seedling families which broke dormancy early, little disparity (0–2 days) in date of dormancy break between compartments was noted. Within the late-breaking clones and seedling families, there were, however, marked divergencies (3–9 days); but there was no indication that complete ab-

[1] So-called "break of dormancy" in these studies was based on observed separation of bud scales. As *Populus* buds swell, the imbricate bud scales separate, revealing the transparent portion of the underlying scale. Examination of the plants in the dark compartment was effected by use of weak yellow light which, in addition to the green portion of the spectrum, is reported to be photoperiodically ineffective, at least in the flowering response (Miller, 11).

sence of light was more inhibiting to the break of dormancy than continuous light.

Date of appearance of the first unrolled leaf was also recorded in these studies. In most cases the flattening process was not complete in the plants subjected to the dark treatment.

Subsequent growth of the plants in darkness gave rise to the typical morphological modifications associated with etiolation, i.e., reduction in leaf size, marked elongation of the shoot with the development of a hook at the end, inhibited diametral growth, and loss of the erect habit (FIG. 8).

FIG. 8. 1-year seedlings of *P. trichocarpa* grown for 5 weeks in normal day (*left*); continuous light (*center*); and continuous darkness (*right*). All plants were dormant at the start of the experiment and all broke dormancy 8 to 10 days later.

Results of these studies appear to confirm the conclusion that the photoperiod is ineffective in the break of dormancy or early growth in length of *Populus*. Later, however, a stage in the annual growth cycle is reached when the day length must be greater than a certain minimum in order for height growth to continue. As has been demonstrated, high latitude clones of *P. trichocarpa*, when grown in the natural-day regime at the latitude of Boston, cease height growth on or about the time of the summer solstice. If, however, the photoperiod is lengthened by the addition of artificial illumination, they continue to grow, ceasing only when the day length again falls below the critical minimum. The role of the photoperiod in the annual growth cycle of *Populus* thus appears to be primarily effective in the timing of physiological processes concerned in the onset of dormancy.

Diametral Growth Cessation

On the basis of weekly recordings of height and diametral increment made on representatives of various *Populus* species in the plantations at Weston and elsewhere during the 1952 season, it is clear that diametral growth is always terminated after height growth ceases. Interclonal differences in the length of time between height and diametral growth cessation ranged from ca. 10 to 30 days; but there appears to be little evidence from these data to suggest that diametral growth cessation is independently controlled by the photoperiod. A more likely explanation seems to be that cessation of growth in diameter is simply one of the final, and perhaps more or less automatic, steps in the dormancy process.

INHERITANCE OF THE PHOTOPERIODIC RESPONSE

The broad and continuous range in time of height growth cessation which characterizes the behavior of the various ecotypes in these studies, suggests that a large number of genes are involved in the photoperiodic reaction. Further indications of multiple factor inheritance are contained in the records on height growth cessation for the offspring and parents of a north-south cross included in the 1951 studies. Under the influence of either the normal- or long-day regime, the progeny ceased height growth at a time intermediate to that of their parents (Table 2).

TABLE 2

NORTH-SOUTH CROSS
DATE OF HEIGHT GROWTH CESSATION FOR PARENTS (183A × 118) AND PROGENY (1599 AND 1600)

Clone No.	Lat. of origin	Date of Height Growth Cessation, 1951	
		Normal-day Plot	Long-day Plot
183A	58–30	8/10	9/15
118	46–50	9/12	10/3
1599		8/25	9/21
1600		8/24	9/20

PRACTICAL AND THEORETICAL SIGNIFICANCE OF THE PHOTOPERIODIC GROWTH RESPONSE

Seed Source

Although it would be unwise on the basis of our present limited knowledge to extend the results of these studies to all ligneous species, several practical generalizations concerning the photoperiodic response in trees and its importance in seed source problems may be noted.

(1) The utilization of seed from northern long-day races for planting in

southern latitudes of long growing season will result in early seasonal growth cessation and consequent dwarfing. Such seed sources should obviously be avoided for the establishment of forest plantations from which maximum production of wood or fiber is desired. On the other hand, such seed sources might prove suitable for the establishment of protection forests in short growing season habitats at high elevations in southern latitudes. The typically small annual increment of northern races when grown in a short-day environment might even make them suitable for special horticultural uses.

(2) Seed derived from ecotypes native of the short growing season, high-altitude habitats of mountainous areas in the low latitudes may be expected to react in a manner similar to northern long-day types and should therefore be avoided as seed sources for forest plantations at the same or more southern latitudes. Such sources of seed may, however, prove highly desirable for introduction into certain long-day environments in northern latitudes having suitably long growing seasons. Support for this generalization is attested by the long history of successful North American tree introductions into the maritime countries of Europe. Conversely, movement of long-day races of native European species into the United States has not met with notable success.

(3) Ecotypes native of long growing season habitats in any particular latitude should be avoided as seed sources for short season habitats at the same latitude because of their susceptibility to early autumn frost damage. For the same reason, such seed sources cannot be successfully moved northward into a long-day environment.

The problem of selecting suitable seed sources of any species for introduction into another environment must obviously take into consideration numerous other environmental factors and genetic characteristics. The above recommendations may be found useful, therefore, only to the extent that they may contribute to limiting the field of search for desirable genotypes. Final decisions on adaptability of the proposed introduction to the new habitat must be based on the observed interaction that results between the introduced genotype and all the factors of its new environment.

Breeding

Because of its fundamental role in the vegetative growth cycle, the photoperiodic response should obviously be a matter of primary concern to the tree breeder. As a means of increasing the net yields of wood or fiber, gene combinations nicely adapted for full utilization of the growing season in a particular habitat, may well prove to be quite as promising as a search for heterotic hybrids.

In view of the probably high genetic diversity of the photoperiodic response in wild tree populations occupying a wide diversity of habitats, initial concern should be directed to the selection of suitable parental materials. This is especially true in F_1 breeding programs and may, to a large extent, explain the unsatisfactory results that have been obtained

by various workers through the selection of parental stocks based on their taxonomic identity and availability, rather than their genetic quality.

Since the photoperiodic response appears to be controlled by a large number of factors, the production of a wide-ranging, transgressive series of photoperiodic types may be expected in F_2 populations. Theoretically, by the initial use of parental ecotypes which give reactions approaching the extremes in day-length response, an F_2 will result which may be expected to contain gene combinations adaptable to almost any growing season length at any latitude.

SUMMARY

For the purpose of studying ecotypic variation in *Populus*, a living collection representative of the ranges of various species in this genus was undertaken in 1947 by the Maria Moors Cabot Foundation for Botanical Research. The studies here reported are concerned primarily with the influence of the photoperiod on time of height growth cessation as observed in the various test areas located in the vicinity of Boston, Massachusetts.

Marked variation in the time that height growth stopped was observed between clonal lines of single species when grown in the same day-length regime and otherwise uniform environment. Analysis of these data revealed that the time of height growth cessation was inversely correlated with the latitude of origin of each clone. Among clones native of uniform day-length zones, the time at which height growth ceased was directly correlated with the length of the frost-free season prevailing in the native habitat of each clone. On the basis of these observations, the conclusion is made that adaptation of *Populus* species to various habitats differing in length of frost-free season is effected by a genetic mechanism which controls the duration of their seasonal period of growth. The photoperiod, which is the only factor of the environment with a uniform seasonal variation that is constant from year to year, functions as the timing device for this mechanism.

Modifications in time of height growth cessation were effected by exposing ramets of various clones to artificially lengthened or shortened photoperiods in otherwise uniform environments. The time of height growth cessation was thus demonstrated to be the result of an interaction between the individual's genotype and the photoperiod. Also observed were other intraclonal modifications in time of height growth cessation that could not be attributed to photoperiodic response. Differences in temperature, available nitrogen, intensity of cultivation, and various other factors are believed to exert a modifying influence on the time that height growth ceases.

Hybrids between clones of northern and southern origin gave a photoperiodic response intermediate to the responses of the parents. These results, and the widely varying photoperiodic responses shown by the various ecotypes used in these studies, indicate that the number of genes involved in the photoperiodic reaction is large.

Experiments on the break of dormancy in the spring indicated that temperature rather than photoperiod is the major factor controlling the initiation of new growth after the period of winter dormancy.

Several practical generalizations concerning the photoperiodic response in trees and its importance in seed source problems and in breeding are noted.

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NOTES ON THE FLORA OF CHINA, III

SHIU-YING HU

With two plates

CRITICAL NOTES on ambiguous binomials concerning the Chinese flora, additional information regarding certain Chinese plants, and the proposal of eight new species, four new varieties, and two new combinations are presented in this paper. Unless identified by (G), indicating that the material is deposited in the Gray Herbarium, all the specimens cited are to be found in the Herbarium of the Arnold Arboretum.

Clematis angustifolia Auct.

Jacquin in 1762 [1] published the species *Clematis angustifolia*, from the coast of southern Europe. According to his description the species was a glabrous vine with pinnate leaves and linear leaflets. Pallas in 1776 described *Clematis hexapetala*, an erect plant with tomentose perianth from eastern Siberia in the regions of the Argun and Onon Rivers. In 1786 Jacquin, probably on account of the shape of the leaf segments, doubtfully amalgamated these geographically widely separated and morphologically manifestly different species. In the discussion of his *Clematis angustifolia* he wrote as follows, expressing his doubt: "An haec eadem cum Ammaniana planta, a Pallasio citata, sit, dubito, quum nostra sit glabra tota, Ammanius vero dicat caules superius lanuginosos . . ." In the same year, under the name *Clematis angustifolia*, he published a colored plate illustrating a plant which he described as erect and with pinnate recurved leaves and linear-lanceolate leaflets. Judging from this illustration and description, Jacquin's concept of his own *Clematis angustifolia* had, by this time, changed from a climbing glabrous vine growing on the coast of southern Europe to an erect pubescent plant occurring in the mountains of central Siberia, for in the Gray Herbarium there is a specimen collected by Schschukin in Irkutsk which matches Jacquin's illustration in every respect. This illustration of Jacquin's has been very misleading, for in the last two centuries botanists who named plants by matching them with illustrations have identified all members of that heterogeneous group of erect herbaceous perennial *Clematis* from North China, Manchuria, Korea, and Eastern Siberia as *Clematis angustifolia* Jacq. Meanwhile most authors who have published accounts of the flora of eastern and northeastern Asia have indiscriminately applied such identifications. Now, both in the herbaria and the literature, we have this oriental taxon carrying an occidental binomial. As Jacquin's species was first published as a climbing

[1] Enumeratio Stirpium Plerarumque, quae Sponte Crescunt in Agro Vindobonensi, Montibusque Confinibus 310.

plant growing on the coast of southern Europe, the application of that binomial should be limited to plants of that region, in spite of the fact that Jacquin later changed the concept of his species. A. P. De Candolle in 1817 (Regni Vegetabilis Systema Naturelle 134, 154) treated *Clematis maritima* Linn. as a variety of *Clematis flammula* Linn. var. *maritima* (L.) DC. in one place and later used it again as a synonym of *Clematis angustifolia* Jacq. In so doing, he seems to have given us a hint that Jacquin's original *Clematis angustifolia* might have been a *Clematis flammula* Linn. var. *maritima* DC., since *Clematis flammula* Linn. is a vine with pinnatisect leaves, and the variety, *C. flammula* Linn. var. *maritima* (L.) DC., has linear segments. This vine habit and the pinnatisect leaves with linear segments are distinguishing characters which Jacquin at first ascribed to his *C. angustifolia*. In the herbarium of the Arnold Arboretum there is a collection from Yeste, Spain, labeled *C. flammula* Linn. var. *maritima* (L.) DC. This specimen represents a glabrous vine with pinnatisect leaves. The linear segments of these leaves appear similar to those of some form of the Chinese elements. It is very likely that this represents the true *C. angustifolia* Jacq., which is very different from the taxon of northeastern Asia, which should be designated as *Clematis hexapetala* Pallas.

Hayata in 1913 overlooked Jacquin's binomial and published a *Clematis angustifolia* from Formosa. This species was originally described as *Clematis leschenaultiana* DC. var. *angustifolia* Hayata in Jour. Coll. Sci. Univ. Tokyo **30**: 16. 1911. It represents a vine with densely tomentose stems and leaves. The leaves are trifoliate with ovate or oblong-lanceolate leaflets which are remotely serrate. The achenes of this species are fusiform. *Clematis leschenaultiana* DC. was originally described from Java. It has been recorded from the Philippines, Formosa, and the warmer regions of the Chinese mainland, as well as from the western Malaysian area. After comparing specimens collected within this wide range I have decided that the Formosan material is not specifically distinct.

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CHINA: Chili [Hopei]: Hsiao-wu-tai shan, *T. N. Meyer 92*; Peking, *S. W. Williams*, Aug. 1876 (G); Hsing-lung shan, *J. C. Liu 622*.

EASTERN SIBERIA AND MANCHURIA: Kirin, *F. H. Chen 182* (G); Dairen, Chinchou, *P. H. Dorsett & W. J. Morse 5937* (G); Harbin, *P. H. & J. H. Dorsett 3292* (G); Nertschinsk [Nerchinsky], *F. Karo* (Plantae Dahuriae) *152c* (ISOTYPE of *Clematis angustifolia* Jacq. *β breviloba* Freyn); Blagowjestschensk, *F. Karo 113b*; Chabarovsk [Khabarovsk], *V. Komarov 706*; Khinganskia, *D. Litvinow 326, 1015*; [Ta-ho-shang shan], *K. Kobayashi*, June 19, 1933; Suifenho, *B. V. Skvortzov*, July 10, 1926; Greater Khingan, Djalautins, *B. V. Skvortzov*, July 27, 1938. Mukden [Moukden], *E. H. Wilson 8818*.

Pallas was the first post-Linnaean botanist who described and illustrated the northeastern Asian erect herbaceous perennial *Clematis* and named it *C. hexapetala*. The leaf of his plant is "per caulem opposita, adscendentia, pinnata: foliolis duris venosis, marginatis, acutis, imi paris ramoso-quadrifidis, superioribus lanceolatis bifidisque, terminali tripartito." The segment of the perianth is "oblonga, extus tomentosa." Plants so characterized had been recorded from Manchuria, northern Korea, and the North China Highlands extending from Long. 108° E. and Lat. 34° N. northeastward to Long. 122° E. and Lat. 40° N. Unfortunately, on account of Jacquin's changed concept of his European species of *C. angustifolia* and his misleading illustration of 1776, this taxon has appeared as *C. angustifolia* Jacq. in botanical literature, especially in that concerning the flora of North China.

Clematis hexapetala Pallas is essentially an upland species growing on grassy mountain slopes. Its distribution is very interesting. So far as our material and records show, it has never been collected west of Long. 103° E. nor south of Lat. 34° N. Its range forms a U-shaped area on the map, with Khabarovsk and northern Korea on the curve, northern Manchuria, Dahuria, and the Lake Baikal area on the northern arm, and with southern Manchuria and the North China Highlands on the southern arm.

The material collected within this range exhibits a definite pattern of variation in the size and shape of the ultimate segment of the pinnatisect leaves. Some of these are linear, measuring up to 5 cm. long and 5 mm. wide in the middle, while others are lanceolate, up to 10 cm. long and 10 mm. or more wide in the middle. Since 1895 many trinomials have been

proposed for the different forms of this variation. Although in the original description the measurements of the ultimate segments of the leaves of typical *C. hexapetala* Pallas were not given, and the type material is not accessible to me for comparison, from Pallas' illustration I am inclined to think that he definitely had a narrow-segmented form with segments 2.5–5 cm. long and 3–5 mm. wide at the middle, and acute at the apex.

When Freyn described his varieties, he stated for *C. angustifolia* Jacq. *α longiloba*, "Die Blätter doppelt gefiedert, mit lineal-lanzettlichen Abschnitten; letztere 8–10 mal länger als breit (4–6–10 mm.). Die Blüten bis 5 cm. im Durchmesser, die jungen Sepalen aussen dickt filzig wollig." For his *C. angustifolia* Jacq. *β breviloba* he gave no measurements but simply added, "wie vorige, aber die Blattabschnitte bei gleicher Breite viel kürzer." Here in the herbarium of the Arnold Arboretum there is an isotype, *F. Karo 152c*, for the latter variety. The size and shape of the ultimate segments of the pinnatisect leaves are identical with those shown in Pallas' illustration. Freyn probably did not realize that Nerchinsky, the locality where *Karo 152c* was collected, lies between the rivers Argun and Onon, the type locality of *C. hexapetala* Pallas. The morphological identity and the geographical coincidence lead me to decide that Freyn's *C. angustifolia* Jacq. *β breviloba* is identical with the typical *C. hexapetala* Pallas. The trinomials proposed by the Japanese botanists have been interpreted as synonyms of *C. angustifolia* Jacq. *β breviloba* Freyn by Nakai. They are here treated as synonyms of *C. hexapetala* Pallas.

Pritzel in 1900 recorded this species under the name of *C. angustifolia* Jacq. from T'ai-pa-shan of southwestern Shensi, as represented by *Giraldi 865*. If his identification is dependable, this collection marks the southernmost limit in the range of distribution for the species. As I have not seen Giraldi's specimen, I am not sure whether it actually belongs here or not.

Clematis hexapetala Pallas var. **longiloba** (Freyn) comb. nov.

Clematis angustifolia Jacq. *α longiloba* Freyn in Oesterr. Bot. Zeit. **45**: 59. 1895.

CHINA: Chili [Chihli, Hopei]: Peking, Western Hills, *P. H. Dorsett & W. J. Morse 7035*; same locality, *Bretschneider* in 1881 (ex Herb. F. B. Forbes 1807); Kiang-hsuai ho, *T. F. King 171*; San-tun-ying, *F. N. Meyer 91*; Hsiao-wu-tai shan, *F. N. Meyer 1352*; same locality, *C. W. Wang 61450*; Wei-chang, *Wm. Purdom 44*; without precise locality, Father *Chanet 28*. Shansi: central part of the province, Lu-yah shan, H. Smith's collector, *Lao Ch'in 8147*.

EASTERN SIBERIA OR MANCHURIA: Zejshaja Pristan am Zeaflusse, *F. Karo 334*, July 1899; Blagovesczensk, *F. Karo*, July 16, 1904; Amur, super et medius, *Korskinsky* in 1891 (G); Ircutsk [Irkutsk], *Schschukin* (G); Moukden, *J. Webster* in 1887 (G); Dahuria, *Turczaninow 8*, Nov. 1859 (G).

KOREA: Pyengyan, *Mrs. R. K. Smith*, July 5, 1937.

This variety is characterized by the larger leaf segments, which are 10–15 mm. wide, attenuated at both ends, acute, rarely obtuse at the apex, sparsely villose on the principal nerves, especially beneath, glabrescent

later in the season. This variety has been introduced into cultivation. I have seen material from Jewell Nursery, Lake City, Minnesota, which is identical with our spontaneous collections. In North China the plant grows on grassy slopes along the dry hillsides. Its white flowers appear in June and July. The obovate achenes are 5 mm. long, 3.5 mm. wide, compressed, villose, and with a persistent densely villose curved style up to 3.5 cm. long.

Clematis hexapetala Pallas var. **smithiana** var. nov.

Herba erecta perennis, 20–30 raro usque 60 cm. alta; foliis pinnatisectis, segmentis ultimis lanceolatis, 1.5–3 cm. longis, 3–7 mm. latis, apice obtusis apiculatisque, subtus villosis, inflorescentiis subpaniculatis, perianthiis lanatis, segmentis oblanceolatis, 1 cm. longis, 3 mm. latis, antheris oblongis, 1.5 mm. longis, carpellis albo-villosis.

CHINA: Shansi: Yün-ch'eng, Chung-t'iao shan, *H. Smith 6039* (TYPE); Huo hsien, *T. Tang 1010.*

This is a dwarf variety which is usually 20–30, rarely up to 60 cm. high at the flowering stage. It can easily be distinguished from all other varieties of this species by its villose lower leaf-surface. It occurs in southern Shansi at an altitude of 1850 meters. The white flower appears in July.

Clematis hexapetala Pall. var. **tchefouensis** (Debeaux), comb. nov.

Clematis angustifolia Jacq. var. *tchefouensis* Debeaux in Act. Soc. Linn. Bordeaux **31:** 117 (Fl. Tché-fou 22). 1877.
Clematis angustifolia sensu Faber in Denkschr. Entwickel. Kiautschou 31. 1898. — sensu Rehder in Jour. Arnold Arb. **4:** 185. 1923, pro parte, non Jacquin, 1762.

CHINA: Shantung: Tche-fou [Chefoo, Chih-fou, Yen-t'ai], *O. Debeaux* (ISOTYPE of *Clematis angustifolia* Jacq. var. *tchefouensis* Debeaux); Tsingtao, Li-chuan, *C. Y. Chiao 2979*; near coast, *A. Jacot*, July 1, 1927; Lao shan, 33 miles south of Tsaingtao, *C. Y. Chiao 2691.*

This variety was originally described on the basis of material collected from the north shore of the Shantung Peninsula. Additional material has proved its rather extensive range, extending to the southern end of the peninsula. It can be distinguished from typical *Clematis hexapetala* Pall. by its subglabrous perianth, which is 2–2.5 cm. in diameter at anthesis.

Clematis hexapetala Pall. var. **insularis,** var. nov.

Herba erecta, caudicibus 1 m. altis, 4 mm. crassis, foliis pinnatisectis, segmentis lobatis vel partitis, ultimo lanceolato, 3–6 cm. longo, 8–13 mm. lato, apice obtuso mucronatoque; floribus subpaniculatis, pedicellis 5–8 cm. longis, perianthiis glabrescentiis, 2.5 cm. diametro.

CHINA: Shantung: Tsingtao, Tsingtao Island, *C. Y. Chiao 2521* (TYPE).

This erect, herbaceous, broad-segmented variety is endemic to a small island on the southern coast of the Shantung Peninsula, where it grows on sandy slopes at sea level. Its white flowers appear in mid-June. Its leaf-

segments resemble those of *C. hexapetala* Pall. var. *longiloba* (Freyn) S. Y. Hu, but the latter taxon can easily be distinguished by its white lanate perianth and sparsely villose nerves on the lower surface of the leaves, while the perianth of this variety is glabrescent and the leaves entirely glabrous.

Clematis hexapetala Pall. var. **elliptica** var. nov.

Clematis angustifolia sensu Finet & Gagnepain, Contrib. Fl. As. Or. **1**: 21. 1905, pro parte. — sensu Loes. in Beih. Bot. Centralbl. **37** (Abt. 2): 112. 1919, non Jacquin, 1862.

Herba erecta perennis; foliis pinnatisectis, praeter nervos subtus glabris, segmento ultimo lanceo-elliptico, 1.5–3 raro usque 5 cm. longo, 4–5 raro usque 8 mm. lato, apice obtuso mucronatoque; perianthiis glabrescentiis.

CHINA: Shantung: Tsingtau [Tsingtao], *Zimmerman 205* (TYPE), *448*.

This variety can be distinguished by its very deeply cut lanceo-elliptic segments of the leaves which are obtuse at the apex. In general appearance it resembles *C. hexapetala* Pall. var. *smithiana* S. Y. Hu of southern Shansi, but the latter variety has a lanate perianth and villose lower leaf surfaces.

Freyn in 1895, on the basis of *F. Karo 125b* collected from Nertschinsk [Nerchinsky], described a form which he named forma *stenophylla*. According to his description, the segments of the leaves are up to 6 cm. long and only 1 mm. wide. In the Gray Herbarium of Harvard University there is a fruiting specimen, *T. Y. Cheo & L. Yen 98*, collected from Feihsien of Shantung Province, of which the segments of the leaves are 5–9 cm. long, 3 mm. wide. Flowering material of the narrow-segmented form from the latter region is awaited for its identity.

Tinospora craveniana sp. nov. (*Pl. I, fig. 6*).

Frutex scandens, ramis striatis sulcatisque, 2–3 mm. diametro, hornotinis hirsutis, internodiis 7–10 cm. longis; foliis tenuiter chartaceis, sagittato-ellipticis, 5.5–11.5 cm. longis, 3–5 cm. latis, basi sagittatis, interstitio inter apices auricularum 1.5–2.5 cm. longo, apice acuminatis, acumine 5–8 mm. longo, integris, praeter nervos glabris, nervis primariis 5, palmatis, nervis secundariis laxe reticulatis, utrinque prominulis, petiolo 2.5–3.5 cm. longo, hirsuto; inflorescentiis racemosis; ♂ racemis fasciculatis, pedunculis gracilibus, 15 mm. longis, hirsutis, rhachibus 4 cm. longis, bracteis lanceolatis, 1–2 mm. longis, pedicellis 12–30 mm. longis, sparse hirsutis, prophyllis 1 vel 2; floribus 3-meris, sepalis 6, glabris, extimis oblongis, 2 mm. longis, intimis lineari-oblongis, 4–5 mm. longis, 1 mm. latis, apice acutis; petalis 6, carnosis, apice suborbicularibus, basi cuneatis, 2 mm. longis; staminibus 6, 3 mm. longis, thecis oblongis, 1 mm. longis, rimis lateralibus dehiscentibus; ovario rudimentario minuto, globoso; ♀ racemis solitariis, pedunculis 4–5 cm. longis; floribus ignotis; fructibus subglobosis, 9 10 mm. diametro, endocarpiis osseis, subhemisphaericis, 7–8 mm. diametro, ventro excavatis, dorso lineis obsoletis, inconspicuis tuberculatis.

CHINA: Kiangsi: Hwang-kong shan, *Y. K. Hsiung 6402* (TYPE, fruit). Szechuan: Mt. Omei, *T. T. Yü 563* (TYPE, staminate flower).

The outline of the anterior portion of the leaf of this species appears to resemble that of *T. malabarica* (Lam.) Miers., but the base of the leaf of the latter species is cordate, not sagittate. The indumentum on the nerves of the lower surface and the sagittate leaf-base of *T. craveniana* suggest relationship with *T. sagittata* (Oliver) Gagnep., but the latter species has linear-lanceolate leaves, smaller flowers with the sepals measuring only 2.5–3 mm. in length, obtuse or rounded at the apex, and suborbicular anthers.

This species is named in honor of Miss Mary G. Craven, who retired in January 1953 after forty-eight years of service in the Herbarium of the Arnold Arboretum of Harvard University. Her skillful handling of the specimens has established a monument to her care of the material as well as to her friendship and association with all who have done taxonomic research in this herbarium, from the days of its founder, Charles S. Sargent, up to the present.

Tinospora imbricata sp. nov. (*Pl. I, fig. 2*).

Tinospora capillipes sensu Chun in Sunyats. **4**: 176, *fig. 34*. 1940. — sensu Yamamoto in Taiwania **1**: 32. 1948, pro parte, non Gagnepain, 1908.

Frutex scandens, ramulis striatis, 2.5 mm. diametro, sparse hirsutis, internodiis 7–13 cm. longis; foliis chartaceis, ovato-oblongis, 12–14 cm. longis, 4–4.8 cm. latis, basi cordatis, lobis auriculatis, imbricatis, apice caudatis, acumine 2 cm. longo, supra glabris, subtus praeter nervos glabris, nervis primariis 7, palmatis, utrinque elevatis, nervis secundariis laxe reticulatis, utrinque conspicuis; petiolo 7 cm. longo, hirsutis, basi tortile; floribus ignotis; infructescentiis subracemosis, pedunculis 3.5–9.5 cm. longis, glabrescentibus, pedicellis 9–12 mm. longis, stipite ovarii 2–5 mm. longo; fructibus rubris, subglobosis, 8–9 mm. diametro, endocarpiis pergameis, 7 mm. longis, 8 mm. latis, ventro excavatis, dorso lineis obscuris, ceterum inconspicuo-rugosis.

CHINA: Kwangsi: Yao-shan, *C. Wang 40521* (TYPE).

This species occurs along the streams in central Kwangsi at altitudes of about 1300 meters. Its red fruits remain on the vine in December. Gagnepain in 1908 described *T. capillipes* on the basis of Balansa's collection from Tonkin.

The type of *T. capillipes* represents a staminate plant which has pubescent sepals. I have seen no specimen of this species. Judging from Gagnepain's illustration (Fl. Gén. Indo-Chine 1: 133. *fig. 14, 11*. 1908), that species is characterized by its ovate leaves with sagittate bases. The basal lobes are rounded and are far apart. Chun in 1940 interpreted *C. Wang 40521* as *T. capillipes* Gagn., but Wang's collection has ovate-oblong leaves with imbricate basal lobes and represents a taxon very different from Gagnepain's species. Yamamoto did not see Wang's collection. In

recording the occurrence of *T. capillipes* Gagn. in Kwangsi he simply adopted Chun's interpretation.

Tinospora intermedia sp. nov. (*Pl. I, fig. 5*).

Frutex scandens, ramulis vetustioribus longitudinaliter rimulosis, hornotinis hirsutis; foliis chartaceis, sagittato-oblongis, raro sagittato-ovatis, 7–11 cm. longis, 3.5–4.5 cm. latis, basi sagittatis, interstitio inter apices auricularum 3.5 cm. longo, apice acuminatis, acumine 6–8 mm. longo, apiculato; inflorescentiis staminatis fasciculatis, pedunculis 2–3.5 cm. longis, bracteis ovatis, ciliatis, 1–1.5 mm. longis, pedicellis 1–1.5 cm. longis, prophyllis 1 vel 2, ovatis, apice ciliatis, cum pedunculis glabrescentibus; sepalis 6, glabris, extimis ovatis, 1–2 mm. longis, intimis oblanceolatis, 3 mm. longis, petalis 6, carnosis, suborbicularibus, apice truncatis; staminibus 6, petalis longioribus, antheris subglobosis, 0.5 mm. diametro; infructescentiis paniculatis, pedunculis 9 cm. longis, fructibus ellipsoideis, 8 mm. longis, 7 mm. diametro, apice apiculatis, endocarpiis pergameneis, ventro excavatis, dorso ceterum lineis conspicuo-tuberculatis.

CHINA: Szechuan: Mt. Omei, *C. Y. Chiao & C. S. Fan 263*; same locality, *C. L. Chow 5777*; *W. P. Fang 16320* (TYPE, staminate flower), *17522* (TYPE, fruit); *W. K. Hu 8803* (sterile); *T. T. Yü 296*.

The leaves of this species appear to resemble those of *T. craveniana* S. Y. Hu in size and texture, but the basal lobes of the latter species point backward and its fruit has a bony rugose endocarp, while the basal lobes of this species all point outward and the endocarp is pergameneous and conspicuously tuberculate. The fruit characters suggest relationship with *T. szechuanensis* S. Y. Hu. Occasionally a few leaves of certain specimens, such as *Chiao & Fan 263*, are short and broad, appearing sagittate-ovate. This character suggests some relationship with *T. capillipes* Gagnepain, which has pubescent sepals. On account of its resemblance to several species in different respects, it is here treated as an intermediate species.

Tinospora szechuanensis sp. nov. (*Pl. I, fig. 1*).

Frutex scandens, ramis striatis et sulcatis, 2.5–3 mm. diametro, hornotinis hirsutis, internodiis 6–7 cm. longis; foliis subcoriaceis, integris, sagittatis, 10–13 cm. longis, 4–4.5 cm. latis, basi sagittatis, interstitiis inter apices auricularum 5.5 cm. longis, apice acuminatis, acumine 15–20 mm. longo, cuspidato, supra glabris, subtus praeter nervos glabris, nervis primariis 5, palmatis, utrinque elevatis, nervis secundariis laxe reticulatis, supra obscuris, subtus prominulis; petiolo 5.5–6 cm. longo, glabrescente; floribus ignotis; infructescentiis paniculatis, pedunculis 9 cm. longis, axibus secundariis 10–15 mm. longis, pedicellis 5–10 mm. longis, cum pedunculis hirsutis; fructibus ellipsoideis, 11 mm. longis, 7–8 mm. diametro, stigmatis subapiculatis, endocarpiis pergameneis, subellipsoideis, 8 mm. longis, 7 mm. latis, ventro excavatis, dorso lineis conspicuo-tuberculatis.

CHINA: Szechuan: Hung-ya, Wa-wu shan, *E. H. Wilson 3528* (TYPE, fruit).

This species is characterized by its subcoriaceous sagittate leaves with the auricles pointing outward, paniculate infructescence with peduncles 9 cm. long, and ellipsoid drupes with conspicuously tuberculate parchment-like endocarp. It is closely related to *T. sagittata* (Oliver) Gagnepain, but the leaves of the latter species are linear-lanceolate, sagittate, with the auricles pointing backward, the infructescences are racemose with the peduncles 4–6 cm. long; and the fruits are subspherical with bony endocarp inconspicuously tuberculate (*Pl. I, fig. 3*).

Tinospora yunnanensis, sp. nov. (*Pl. I, fig. 4*).

Frutex scandens, ramulis striatis et sulcatis, vetustioribus tuberculatis, lenticellis conspicuis, orbiculatis, elevatis, hornotinis hirsutis vel glabrescentibus; foliis subcoriaceis, sagittato-ovatis, 12–14 cm. longis, 4.5–5.5 cm. latis, basi cordato-sagittatis, auriculis rotundatis, interstitia inter apices auricularum 1.5–2.5 cm. longa, apice acuminatis, acumine 11–13 mm. longo, apiculato, utrinque rugosis, praeter nervos subtus glabris, nervis primariis 7, utrinque evidentibus, reticulatis obscuris; inflorescentiis staminatis, ramis vetustis positis, racemosis, racemis solitariis vel fasciculatis, pedunculis 4–5.5 cm. longis, glabrescentibus, bracteis lanceolatis, 2 mm. longis, apice ciliatis, pedicellis 7–10 mm. longis, pilosis; sepalis 6, extimis ellipticis, 1.5 mm. longis, 0.75 mm. latis, intimis unguicularibus, 2 mm. longis, 1.5 mm. latis, glabris; petalis 6, suborbicularibus, basi cuneatis; staminibus 6, filamentis petalis subaequalibus; ovario rudimentario globoso; floribus pistillatis fructibusque ignotis.

CHINA: Yunnan: without precise locality, *H. T. Tsai 53100* (TYPE).

This species is closely related to *T. capillipes* Gagnepain, but the latter species has villose sepals, while those of this species are glabrous.

Chimonanthus salicifolius, sp. nov.

Frutex, ramulis subteretis, puberulis; foliis lineari-lanceolatis, 3–9 cm. longis, 1–3 cm. latis, basi obtusis, apice obtusis vel acutis, subcoriaceis, supra glabra, paulum nitidis, subtus opacis, hirsutis, costa utrinque elevata, nervis lateralibus 5 vel 6 paribus, reticulatis; floribus solitariis, axillaribus, pedicellis brevissimis, 4 mm. longis, bracteolis imbricatis, ovatis, puberulis; perianthiis exterioribus rotundatis, puberulis, interioribus ignotis.

CHINA: Kiangsi: Hsiu-shui, *Y. K. Hsiung 5489* (TYPE).

This species is closely allied to *C. nitens* Oliver, but the latter species has glabrous ovate-elliptic leaves with a long acuminate apex.

Euonymus orgyalis W. W. Smith in Notes Bot. Gard. Edinb. 13: 161. 1921.

CHINA: Yunnan: Si-chour hsien, Faa-doou, *K. M. Feng 12044*; same district, Ma-chia, *K. M. Feng 12502*; Mar-li-po, Huang-jin-in, *K. M. Feng*

13067; Mengtze, *A. Henry 11404*; Ping-pien hsien, *H. T. Tsai 55328, 55345, 60197, 60967, 61020, 61395, 61744, 61778*, and *62446*.

The description of this species was based on a flowering specimen collected by *A. Henry* (*10661*) in southeastern Yunnan at an altitude of 2100 meters. The largest leaf of that material measures only 9 cm. long and is rounded at the base. Additional material from the same general area exhibits variations in the size and shape of the leaves and in the habit of the plant. As we now know it, the larger leaves of this species measure up to 15 cm. long and 7 cm. wide and are oblong-elliptic in shape. *Tsai 55328*, also a flowering specimen, even possesses an evergreen habit. In southeastern Yunnan the plant occurs at altitudes as low as 1300 meters, in ravines, on rocky crevices, or along the streams of the mixed forest zone. It is usually a shrub 2–3 m. high but occasionally appears scandent. The green flowers appear in late May. The specimen collected in early September has very small young fruit, the one collected in mid-October has fruit reaching mature size, and that collected in November has fruit dehiscent by apical slits. The mature fruit is globose, 12 mm. in diameter, with a rough and woody pericarp.

Craibiodendron kwangtungense, sp. nov.

Craibiodendron stellatum sensu Merrill in Lingn. Sci. Jour. 7: 319. 1931, non (Pierre) W. W. Smith 1914.

Arbor sempervirens, 10–12 m. alta, ramulis glabris, lenticellis obscuris; foliis alternis, coriaceis, olivaceo-brunneis, supra nitidis subtus opacis, ellipticis vel lanceolatis, 6–8 cm. longis, 1.8–3 cm. latis, integris, utrinque attenuatis, basi acutis vel cuneatis, apice acutis, obtusis, raro breviter acuminatis, costa supra impressa, subtus elevata, nervis lateralibus 18–22 paribus, supra evidentibus, subtus prominentibus, margine anastomosantibus, reticulatis distinctis, stipulis obsoletis, petiolo 8–10 mm. longo; inflorescentiis racemosis simplicibus, axillaribus, rhachibus 4–5 cm. longis, minute puberulis, bracteis lanceolatis, 2 mm. longis, ciliatis, deciduis; pedicellis 2–3 mm. longis, furfuraceis puberulisque, prophyllis 2, submedio instructis; calycibus cyathiformibus, 2–3 mm. diametro, sparse puberulis, lobis 5, rotundatis, ciliatis; corolla breviter campanulata, glabra; staminibus 10, inclusis, filamentis glabris, antheris basi subsaccatis, dorso muticis; ovario globoso, 1 mm. longo, 5-loculari, stylo columnari, 2 mm. longo; capsulis depresso-globosis, 14 mm. longis, 18 mm. diametro, profunde 5-angulatis, pericarpiis ligneis; seminibus in loculo quoque 12–14, subovoideis, leviter compressis, 2 mm. longis, 2 mm. latis, alis obliquis, 10 mm. longis, 8 mm. latis, rugosulo-striatis.

CHINA: Kwangtung: Ting-wu-shan, *Y. Tsiang 792* (TYPE, flower), *1533*, *1547*; Kwangsi: south of Nan-ning, Seh-feng-dar shan, *R. C. Ching 8293* (TYPE, fruit).

Craibiodendron kwangtungense is a tree 14 meters high with a trunk 30 cm. in diameter. It occurs in southwestern Kwangtung and southeastern Kwangsi at an altitude of six hundred meters. By the lanceolate leaves,

attenuated at both ends, and the glabrous corolla, it can be distinguished from *C. stellatum* (Pierre) W. W. Smith, which has oblong leaves rounded at the apex, and pubescent corolla. It is also related to *C. henryi* W. W. Smith, which has long acuminate leaves, paniculate racemes, smaller fruits which are only 8 mm. long and 10 mm. in diameter.

Craibiodendron kwangtungense var. **frutescens,** var. nov.

Frutex 2–3 m. altus, ramulis puberulis; foliis oblongo-ellipticis, 5–6 cm. longis, 2.5–3.5 cm. latis, apice obtusis vel abrupte brevi-acuminatis, racemis puberulis simplicibus, axillaribus.

CHINA: Kwangtung: Ting-wu-shan, *W. Y. Chun 6363.* Kwangsi: Shang-sze, Shap-man-taai shan, *W. T. Tsang 22252* (TYPE).

This variety differs from the typical *C. kwangtungense* in habit, being a shrub 2–3 meters high; also it has broader leaves and more pubescent racemes.

Ligustrum subsessile, sp. nov.

Frutex, ramulis robustis, teretis, cineraceis, triannis 5 mm. diametro, longitudinaliter minute rimulosis, lenticellis orbicularibus, cicatricibus foliorum semicircularibus, elevatis, hornotinis 2–3 mm. diametro, internodiis 2–3 cm. longis, ± striatis, in triis sparse pilosis, ceterum glabris, lenticellis conspicuis; foliis subsessilibus, integerrimis, subcoriaceis, ovato-oblongis vel oblongis vel raro suborbicularibus, utrinque rotundatis, 4–9 cm. longis, 3–4.5 cm. latis, glabris, subtus punctatis, costa supra plana, subtus leviter elevata, nervis lateralibus 4 usque 9 paribus, supra obscuris, subtus evidentibus, petiolo 1–2 mm. longo, glabro; floribus ignotis; infructescentiis paniculatis, paniculis compactis, subcylindraceis, 4–6 cm. longis, 2–4 cm. diametro, pedunculis 1.5–2 cm. longis, sparse puberulis, rhachibus subquadrangularibus, in striis sparse puberulis, axibus secundariis 5–15 mm. longis, sparse minute puberulis, pedicellis 1–2 mm. longis, glabris; sepalis persistentibus 3 mm. diametro, lobis 4, rotundatis, glabris; fructibus oblongo-subglobosis, 5–7 mm. longis, 4–6 mm. diametro.

CHINA: Kiangsi: [Hsiu-shiu], Hwang-lung shan, Nung-lung temple, *Y. K. Hsiung 5629* (TYPE).

This species has been reported to be a common shrub in thickets along the streams of the Kiangsi-Hupeh-Hunan border. The specimen cited above was collected in late August. The fruits are still too young for the study of the seed characters. I have not been able to match it with any *Ligustrum* in our collection. The general appearance of the compact inflorescences and of some of the smaller leaves resembles that of those shown in Hooker's illustration (Bot. Mag. 123: *pl. 7519.* 1897) for *Ligustrum coriaceum* Carrière, a species published on the basis of cultivated plants introduced to European gardens by Robert Fortune, reportedly from Japan. But specimens from European and Japanese gardens (such as those from Hort. Vilmorin of France, the Royal Botanic Gardens at Kew in Eng-

land, and the Botanical Garden of Tokyo) which match Carrière's and Hooker's descriptions and illustrations, all have smaller leaves, the smallest ones being 1.5 cm. long, 1 cm. wide, and the largest ones being 4 cm. long. 3 cm. wide. They all have comparatively longer petioles which are 3–7 mm. long. In comparing them with Hsiung's collection from Kiangsi, I conclude that the latter, with its subsessile large leaves, is specifically distinct.

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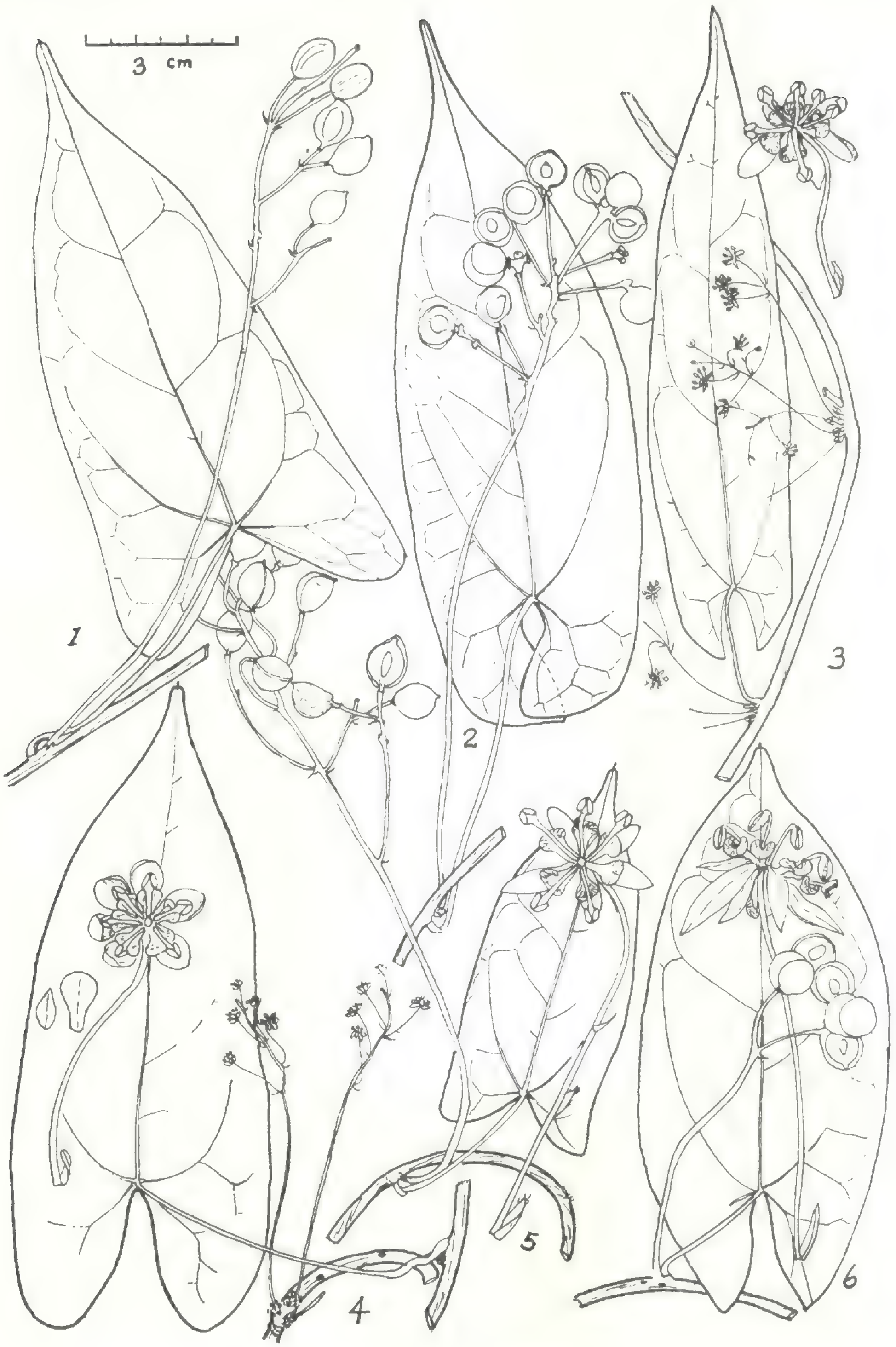
EXPLANATION OF THE PLATES

PLATE I

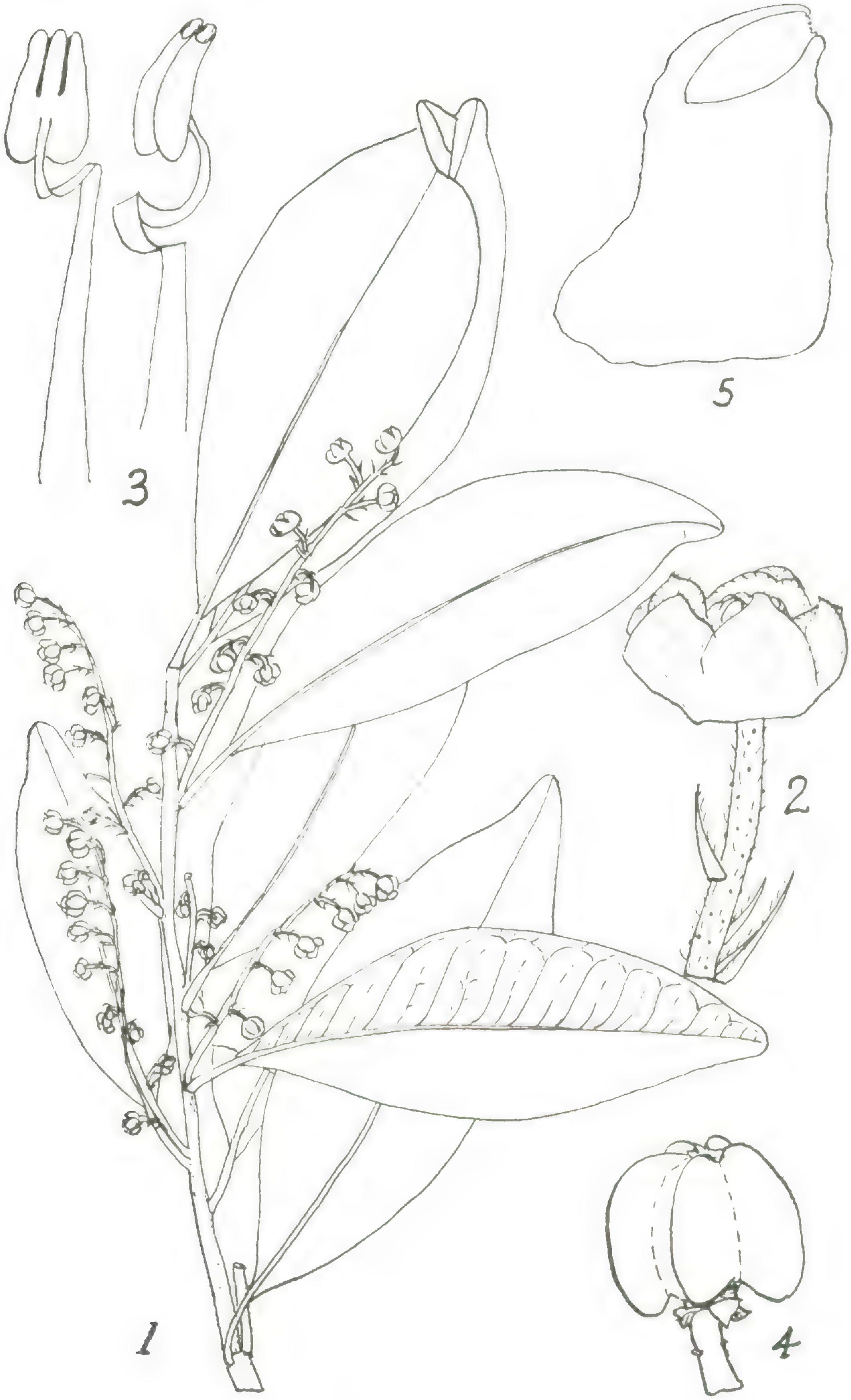
FIG. 1. A habit sketch of a fruiting branch of *Tinospora szechuanensis* showing the basal lobes of the leaf pointing outward. FIG. 2. A habit sketch of a fruiting branch of *Tinospora imbricata* showing the imbricate basal lobes of the leaf. FIG. 3. A habit sketch of a staminate flowering branch of *Tinospora henryi* with a separate flower enlarged 5 times. FIG. 4. A habit sketch of a leafy branch of *Tinospora yunnanensis* and a staminate flowering branch showing the inflorescences on old growth, with a separate staminate flower and a smaller outer and a larger inner sepal enlarged 5 times. FIG. 5. A habit sketch of a fruiting branch of *Tinospora intermedia* with a separate staminate flower enlarged 5 times. FIG. 6. A habit sketch of a fruiting branch of *Tinospora craveniana* with a separate staminate flower enlarged 5 times.

PLATE II

FIG. 1. A habit sketch of *Craibiodendron kwangtungense* showing solitary axillary racemes. FIG. 2. A flower after anthesis (× 10). FIG. 3. Two anthers, dorsal and sublateral view (× 18). FIG. 4. A fruit (× 1½). FIG. 5. A seed (× 5).



SPECIES OF TINOSPORA



CRAIBIODENDRON KWANGTUNGENSE HU

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THE CYPERACEAE COLLECTED IN NEW GUINEA BY L. J. BRASS, IV.*

S. T. BLAKE

With one plate and two text-figures

THIS PAPER COMPLETES the account of the specimens collected by Mr. L. J. Brass during the Archbold Expeditions between 1933 and 1939. As in the previous contributions (Jour. Arnold Arb. **28**: 99–116, 207–229. 1947; **29**: 90–102. 1948), some other specimens are cited. To the acknowledgements made in earlier contributions, I wish to add my thanks to Prof. H. Humbert, Dr. O. Hagerup, Dr. A. Hässler and Dr. H. J. Lam for the loan of types and other material from the herbaria of Paris, Copenhagen, Lund and Leiden respectively, and to Mr. R. H. Anderson for the loan of all specimens of *Scleria* in the Sydney Herbarium.

The genera treated here are *Scirpus*, *Fimbristylis*, *Scleria*, *Diplacrum* and *Uncinia*, and there are some additional notes on genera previously treated. The treatment of the different genera is somewhat unequal, particularly as to the citation of synonyms, but in all cases it is based on fairly extensive revisional work on the Malaysian and Australasian species. The delayed appearance of this paper is due partly to the necessity of examining certain types before some groups of species could be determined satisfactorily.

Herbaria are indicated by the following abbreviations: Brisbane, BRI; Canberra, CANB; Copenhagen, C; Leiden, L; Lund, LD; Melbourne, MEL; Paris, P; Sydney, NSW.

Scirpus Linnaeus

Scirpus ternatanus Reinw. ex Miq. Fl. Ind. Bat. **3**: 307. 1859; Kükenth. Bot. Jahrb. **69**: 259. 1938; Ohwi, Bot. Mag. Tokyo **56**: 204. 1942.

Scirpus chinensis Munro in Seem. Bot. Voy. Herald 423. 1857; Valck. Suring. Nova Guin. Bot. **8**: 705. 1912; Ridl. Trans. Linn. Soc. II, Bot. **9**: 242. 1926; non Osbeck 1753.

* Botanical Results of the Richard Archbold Expeditions. See Jour. Arnold Arb. **29**: 90–102. 1948.

NETHERLANDS NEW GUINEA: Bele R., 18 km. NE. of Lake Habbema, *Brass 11472*, Nov. 1938, alt. 2200 m., large clumps in moist situations on grassy, formerly cultivated slopes; Balim R., *Brass 11677*, Dec. 1938, alt. 1600 m., colonizing loose sand and stones from a landslip; 9 km. NE. of Lake Habbema, *Brass 10993*, Oct. 1938, alt. 2650 m., plentiful in *Equisetum* cover on landslips, large clumps ± 75 cm. high; 9 km. NE. of Lake Habbema, *Brass 10883*, Oct. 1938, alt. 2650 m., open banks of a stream in forest.

The range of this species extends north and west through Malaysia to India, China and Japan.

? **Scirpus strobolinus** Roxb. Hort. Beng. 6. 1814, *nomen nudum*. Fl. Ind. ed. Carey & Wall. 1: 223. 1820, Fl. Ind. ed. Carey 1: 219. 1832.

PAPUA: Western Division: Gaima, Lower Fly R. (east bank), *Brass 8304*, Nov. 1936, loose sand on open foreshores, not common.

The specimens are in flower only and the identification is rather uncertain, though they appear to belong here rather than to *S. maritimus* L., *S. fluviatilis* A. Gray or *S. paludosus* A. Nels. *Scirpus strobolinus* is otherwise known from different parts of Asia, extending south to Assam and Pegu.

Scirpus mucronatus L. Sp. Pl. 50. 1753; K. Schum. in K. Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee 195. 1901; Valck. Suring. Nova Guin. Bot. **8**: 704. 1912; Kükenth. Bot. Jahrb. **59**: 51. 1924, **69**: 259. 1938.

NETHERLANDS NEW GUINEA: Balim R., *Brass 11804*, Dec. 1938, alt. 1600 m., occasional in ditches and grassy pools.

PAPUA: Western Division: Junction of Black and Palmer Rivers, *Brass 6943*, June 1936, common on silt-covered gravel banks in river (det. Uittien). Central Division: Urunu, Vanapa Valley, *Brass 4810*, July–Aug. 1933, alt. 1900 m., plentiful in small swamps on open slopes of valley; Koitaki, *Carr 12283*, May 1935, alt. 1500 ft., swamp in open savannah land, c. 4 ft. tall (herb. Canberra).

A species widely spread over the warmer parts of the Eastern Hemisphere.

Scirpus clemensiae (Kükenth.) Ohwi, Bot. Mag. Tokyo **56**: 203. 1942.

Scirpus clemensiae (Kükenth.) Kükenth. Mitteil. Thüring. Bot. Ver. N. F. **50**: 13. 1943.

Scirpus mucronatus L. subsp. *clemensii* Kükenth. Bot. Jahrb. **69**: 259. 1939.

NETHERLANDS NEW GUINEA: Lake Habbema, *Brass 9069*, August 1938, alt. 3225 m., plentiful in sandy marginal shallows of lake, tufts 40–60 cm. high; Lake Habbema, *Brass 9439*, August 1938, alt. 3225 m., abundant in marginal shallows of lake.

Known also from North-East New Guinea, whence it was originally de-

scribed. The binary combination was made independently by Ohwi and Kükenthal. Ohwi spelled the epithet *Clemensii*, as published in the ternary combination. When Kükenthal made the binary combination, he cited "Scirpus Clemensiae Kükenth., comb. nova. — *Sc. mucronatus* L. subsp. *Clemensii* Kükenth. in Bot. Jahrb. 69.2. (1938) 259." It would appear that the spelling *Clemensii* in the first paper was "an unintentional orthographic error" which was corrected in the later paper, as permitted by Art. 70 of the International Rules, and I have adopted the emended spelling. The plant was evidently dedicated to Mrs. M. S. Clemens.

Scirpus validus Vahl, Enum. 2: 268. 1806.

PAPUA: Western Divison: Gaima, Lower Fly R. (east bank), *Brass 8305*, Nov. 1936, gregarious on open sandy foreshores.

New for Papua; widely spread in the countries around the Pacific Ocean and in the Americas generally. Specimens from New Guinea were formerly identified with the Eurasian *S. Tabernaemontani* Gmel. by Kükenthal in Engl. Bot. Jahrb. **59**: 51. 1924, and by Ohwi in Bot. Mag. Tokyo **56**: 203. 1942. I have accepted Beetle's arrangement of this group of species in Amer. Jour. Bot. **28**: 691–700. 1941.

Scirpus grossus L. f. Suppl. 104. 1781; Valck. Suring. Nova Guin. Bot. **8**: 705. 1912.

PAPUA: Western Division: Gaima, Lower Fly R. (east bank), *Brass 8311*, Nov. 1936, co-dominant with no. *8312* (= *Cyperus malaccensis* Lam.) in extensive sedge communities on open sandy foreshores (det. Uittien).

New for Papua. The species ranges from India to NE. Queensland, and in New Guinea was previously known only from Netherlands New Guinea.

Scirpus crassiusculus (Hook. f.) Benth. Fl. Austral. 7: 326. 1878; Kükenth. Bot. Jahrb. **69**: 258. 1938.

Isolepis crassiuscula Hook. f. Fl. Tasm. 2: 86, *t. 143*. 1860.

NETHERLANDS NEW GUINEA: Lake Habbema, *Brass 9324*, Aug. 1938, alt. 3225 m., gregarious on sand bars in grassland stream; Mt. Wilhelmina, 4 km. NE. of top, *Brass & Meyer-Drees 9984*, Sept. 1938, alt. 3660 m., submerged green masses in shallows of a lake.

PAPUA: Central Division: Mt. Albert Edward, *Brass 4300*, May–July 1933, alt. 3810 m., submerged in large masses on shallows of an alpine lake.

New for both Netherlands New Guinea and Papua. Recorded by Kükenthal, l.c., for North-East New Guinea, but he credited the authorship of the combination under *Scirpus* to Hooker f., l.c. Bentham, l.c., also credited the combination to Hooker. The species is elsewhere known from SE. Australia (including Tasmania) and New Zealand.

The sheet seen of *Brass & Meyer-Drees 9984* has but one spikelet, too immature for dissection, but the facies of the plant is of this species.

Scirpus merrillii (Palla) Kükenth. ex Merr. Enum. Philipp. Fl. Pl. 1: 117. 1925; S. T. Blake, Proc. Roy. Soc. Queensl. **58**: 38. 1947.

Schoenoplectus merrillii Palla in Kneucker, Cyperaceae (excl. Carices) et Juncaceae exsiccatae **8**: *nr. 223.* 1911, in Allgem. Bot. Zeitschr. **17**: Beil. 3. 1911.

NETHERLANDS NEW GUINEA: Lake Habbema, *Brass 9238*, Aug. 1938, alt. 3225 m., associated with mosses, etc., on open seepages.

PAPUA: Central Division: Mt. Albert Edward, *Brass 4364*, May–July 1933, alt. 3680 m., plentiful on wet banks of a small alpine stream; Murray Pass, Wharton Range, *Brass 4725*, June–Sept. 1933, alt. 2840 m., common, wet banks of grassland streams. Eastern Division: Mt. Dayman, *W. Armit* in 1894 (MEL).

New for New Guinea, though it is very likely this species which has been recorded as *S. inundatus* (R. Br.) Poir. by Kükenthal, Bot. Jahrb. **69**: 258. 1938, from North-East New Guinea and by Ohwi, Bot. Mag. Tokyo **56**: 203. 1942, from Netherlands New Guinea. It differs from the polymorphic *S. inundatus* by the constant development of a filiform branched rhizome, well-developed leaves often overtopping the culm, more or less emarginate glumes nearly as broad as long and scarcely if at all mucronate, and with the nut nearly as long as the glume; also it is almost invariably a much smaller, very slender, more or less mat-like plant with mostly only one, rarely two or three spikelets, and the involucral bract is commonly elongated. I have seen other specimens from the Philippine Islands including an isotype (*Merrill in Kneucker Cyperaceae et Juncaceae exsiccatae* **8**, *nr. 223*), south-east Queensland, New South Wales, Victoria, Tasmania and New Zealand.

Scirpus clarkei Stapf, Trans. Linn. Soc. II, Bot. **4**: 244. 1894.

Scirpus pulogensis Merr. Philipp. Jour. Sci. **5 (C)**: 333. 1910; **syn. nov.**
Scirpus pakapakensis Stapf, Jour. Linn. Soc. Bot. **42**: 174. 1914; **syn. nov.**
Scirpus subcapitatus Thw. var. *triangularis* Kükenth. Bull. Jard. Bot. Buitenz. sér. III, **16**: 301. 1940; **syn. nov.**
Scirpus subcapitatus Thw. forma *rigidus* Kükenth., l.c., **syn. nov.**
Scirpus clarkei Stapf var. *pakapakensis* (Stapf) Beetle, Amer. Jour. Bot. 33: 665. 1946; **syn. nov.**

PAPUA: Central Division: Mt. Albert Edward, *Brass 4315*, May–July 1933, alt. 3680 m., forest glades and grassland slopes, common, few plants fertile; Mt. Knutsford, *W. MacGregor* in 1889 (BRI, MEL); summit of the Owen Stanley Ranges, *W. MacGregor* in 1889 (MEL).

New for New Guinea; elsewhere known from the Philippine Islands, Borneo and Sumatra.

F. Mueller, Trans. Roy. Soc. Vict. n.s. 1 (2): 35. 1889, referred MacGregor's specimens to *S. cespitosus* L. (as *S. caespitosus*) with the remark: "Should nevertheless this plant, as a variety or perhaps even as a species, require separation from the genuine S. caespitosus, then the name heleocharoides would be an apt one." Some of the specimens are labelled in

Mueller's handwriting: Scirpus caespitosus Linné var. heleocharoides. This ternary combination has never been validly published, for the phrase quoted cannot be taken as constituting publication of any combination.

The specimens from New Guinea do indeed closely resemble specimens of *S. caespitosus* L., but the leaf-sheaths are fewer, tighter and more rigid, the hard culms are more or less trigonous and less furrowed, the two lowermost glumes are much shorter and more rigid than the others and only shortly pointed, and the nut is narrower. Occasionally also the inflorescence consists of two spikelets. They also resemble some from the Philippine Islands (ISOTYPE of *S. pulogensis*), Borneo (Mt. Kinabalu, the type-locality of *S. clarkei* and *S. pakapakensis*) and Sumatra (general locality of the types of *S. subcapitatus* var. *triangularis* and *S. subcapitatus* forma *rigidus*). *Scirpus clarkei* will probably prove to be conspecific with *S. subcapitatus* Thw. from Ceylon and southern India; of this I have seen only one sheet, an isotype, but it is in flower only.

Beetle, in the paper quoted above, recognised five taxa in a group which he described as *Scirpus* sect. *Paucispicatae* Beetle, l.c., 664. He distinguished *S. clarkei* from *S. subcapitatus* on differences in the number of spikelets and scabridity of the mucro to the leaf-sheaths and lowermost glumes. *Scirpus pakapakensis* was distinguished as a variety of *S. clarkei* by the spikelet not solitary and the stems more or less triangular. He also saw only a single sheet in flower (an isotype) of *S. subcapitatus*. The number of spikelets and shape of the culms are certainly variable, but on the material seen the character of scabridity seems constant. I have not seen material of the other species admitted by Beetle.

F. Mueller, l.c., remarked that "Another Scirpus is contained in the collections, as gathered on Mt. Knutsford and Mount Musgrave; it is an aged state of fructification, and may perhaps belong to the variety fluviatilis of S. maritimus." These specimens are of *Mapania Moseleyi* C. B. Clarke.

Fimbristylis Vahl

No satisfactory account of this genus as a whole has ever been published. The latest account which has any claim to be considered as a general treatment of the genus is Boeckeler's uncritical descriptions of the forms represented in the Berlin Herbarium in Linnaea **37**: 2–56. 1871, **38**: 384–398. 1874. In Kew Bull. Add. Ser. **8**: 107–109. 1908 is a list of species as accepted and arranged by C. B. Clarke, but one of the tragedies in botany is that his extensive manuscript on the family was never published.

The study of the New Guinea collections, the results of which appear on the following pages, was based chiefly on the revision of the Australian species which I commenced in 1932, but which is not yet completed, owing to the numerous difficulties involved, due partly to the need of critically comparing some Australian forms with others described from other parts of the world, of which types were not readily accessible. Little was previ-

ously known of the *Fimbristylis*-flora of southern New Guinea, to which Mr. Brass has added a remarkable number of Australian forms.

For convenience, I have arranged the species under the four sections proposed by Bentham, Fl. Austral. 7: 298–9. 1878, an arrangement which has been fairly generally followed. The type-species of the genus, *F. dichotoma* (L.) Vahl, was arranged under *Dichelostylis* Benth., l.c., 299. but Boeckeler, op. cit. 3. 1841, had previously proposed the name *Eufimbristylis* for the section containing this species.

Sect. **Heleocharoides** Benth.

Fimbristylis setacea Benth. Lond. Jour. Bot. 2: 239. 1843; Valck. Suring. Nova Guin. Bot. 8: 702. 1912.

Fimbristylis acuminata (Retz.) Vahl var. *minor* Miq. Fl. Ind. Bat. 3: 314. 1859.
Fimbristylis acuminata (Retz.) Vahl var. *setacea* (Benth.) Benth. Fl. Austral. 7: 301. 1878.
Fimbristylis acuminata (Retz.) Vahl var. *setacea* (Benth.) Kükenth. Bot. Jahrb. **59:** 47. 1924, **69:** 257. 1938.
Isolepis cochleata Steud. Synops. Cyper. 100. 1855.

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7531A*, August 1936, savannahs, abundant on hard-pans and swamp margins (det. Kükenthal as *Fimbristylis acuminata* (Retz.) Vahl var. *setacea* Bth.); Daru Island, *Brass 6245*, March 1936, abundant in flattened tufts on damp soil in savannah-forests.

New for Papua. The species ranges from Tropical Asia to northern and north-eastern Australia. Kükenthal, 1924, l.c., made a new combination *F. acuminata* (Retz.) Vahl var. *setacea* (Benth.) Kükenth., evidently overlooking Bentham's much earlier combination. But if this form is treated as a variety of *F. acuminata*, then the legitimate trinomial would be *F. acuminata* var. *minor* Miq., l.c. The species is very close to *F. acuminata*, differing chiefly in being smaller in all its parts.

Fimbristylis nutans (Retz.) Vahl, Enum. 2: 285. 1806.

Scirpus nutans Retz. Observ. 4: 12. 1786.

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7843*, Sept. 1936, common on wet grass plains; Wuroi, Oriomo R., *Brass 5750*, Jan.–March 1934, alt. 10–30 m., very plentiful on open savannah.

Not previously recorded for New Guinea, though the species is known to extend from northern and north-eastern Australia to Malaya and China.

Fimbristylis tetragona R. Br. Prodr. 226. 1810; Kükenth. Mitteil. Thüring. Bot. Ver. N. F. **50**: 8. 1943.

Fimbristylis cylindrocarpa Kunth, Enum. 2: 222. 1837.
Fimbristylis arnottii Thw. Enum. Pl. Zeyl. 348. 1864.

Fimbristylis xyroides Arnott ex Thw., l.c., in syn., *nomen nudum*.
Fimbristylis abjiciens Steud. Synops. Cyper. 107. 1855.
Scirpus tetragonus (R. Br.) Poir. Encycl. Suppl. **5**: 98. 1817.
Mischospora efoliata Boeck. Flora **43**: 113. 1860.

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7844*, Sept. 1936, tufted on wet grass plains, plant bluish (det. Svenson).

New for New Guinea; also in southern and eastern Asia and northern Australia.

Fimbristylis dictyocolea sp. nov. (Sect. *Heleocharoides* Benth.). Fig. 1.

Herba perennis, caespitosa, circiter 20–40 cm. alta, fere aphylla. Culmi stricti, erecti, setacei, pluristriati, obscure quinquangulares, glabri, laeves vel minute asperuli, basi haud incrassati. Folia basalia perpauca, setacea, triquetra, lateraliter compressa, glabra, laevia, brevia vel culmum fere adaequantia; folia caulina basi culmi inserta, ad vaginas arctas ore oblique sectas antice late hyalinas tandem reticulatim fissas redacta. Inflorescentia unispiculata, quasi ebracteata. Spicula erecta, pallida, oblonga vel ellipsoidea, utrinque ± acuta, haud angulata, 7–9 mm. longa, 3 mm. lata, multi- et densi-flora. Rhachilla exalata. Glumae undique spiraliter arcte imbricatae, oblongae, apice obtusa rotundatae, muticae, omnino glabrae, dorso late coriaceae uninerves nec carinatae, lateribus membranaceae cellulis parvis breviter oblongis, marginibus etiam apice hyalinae, 4–5 mm. longae, 1–3 imae vacuae crassiores. Stamina 3; antherae lineares, prominule apiculatae, circiter 2 mm. longae. Stylus tenuis, complanatus, basi dilatatus, marginibus minute ciliolatus, circiter 3–3.5 mm. longus; stigmata 3, brevia. Nux straminea, lucidula, obovoidea, late umbonulata, vix stipitata, trigona, leviter tricostulata, minute reticulata verrucosaque cellulis extimis minimis distinctis hexagonis, 1 mm. longa, 0.7 mm. lata.

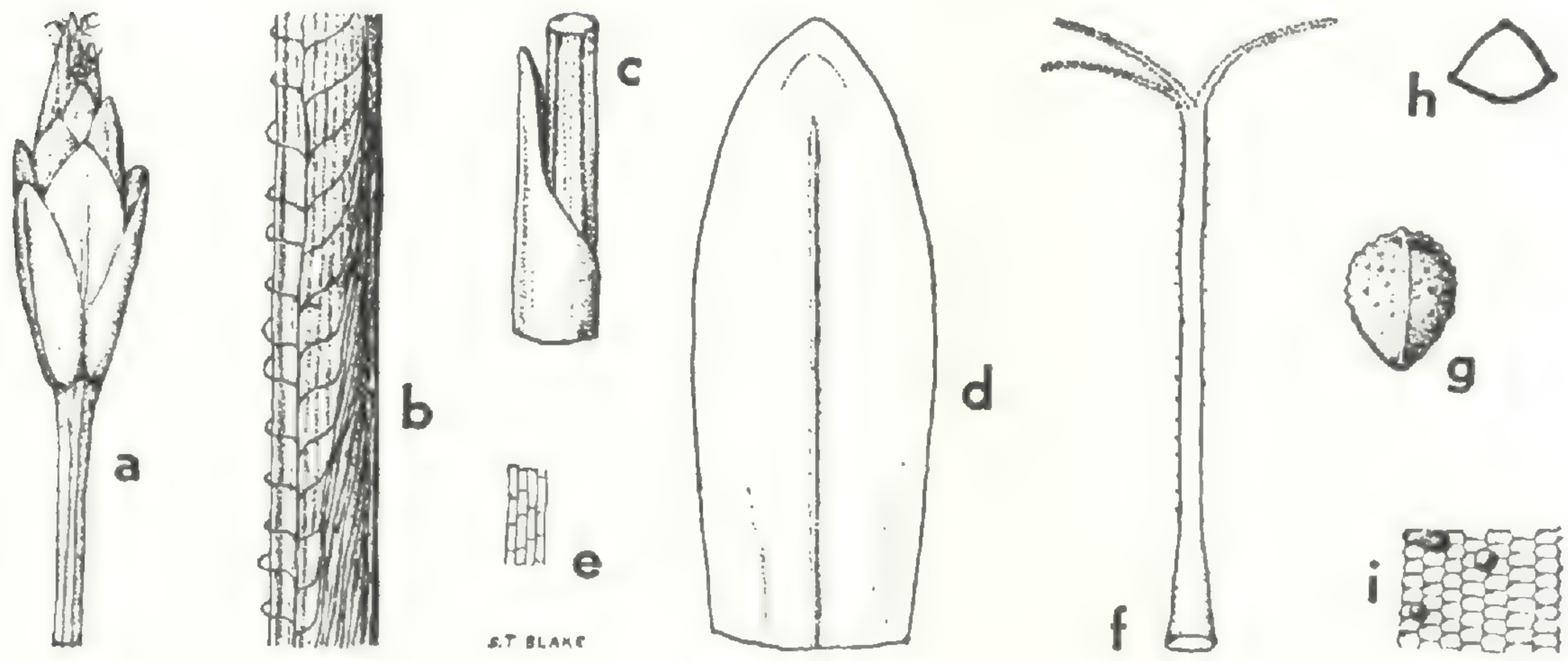

Fig. 1. *Fimbristylis dictyocolea* S. T. Blake: a. upper part of culm with spikelet, × 3; b. middle part, and c. upper part of leaf-sheath, × 3; d. glume, × 10; e. portion of side of glume, × 40; f. style, × 10; g. nut, × 10; h. transverse section of nut; i. surface of nut, × 40. Figures from type.

PAPUA: Western Division: Tarara, Wassi Kussa R., *Brass 8400*, Dec. 1936, abundant on gray soil flat, savannah-forest; Mabaduan, *Brass 6553* (TYPE), April 1936, common in shallow rain-pools in savannah-forests.

Brass 6553 had been determined by Svenson as *F. pauciflora* R. Br., while both it and *Brass 8400*, which is in flower only, were cited by Kükenthal, Mitteil. Thüring. Bot. Ver. N. F. **50**: 9. 1943 as *F. cardiocarpa* F. Muell. The species is certainly allied to *F. pauciflora* R. Br., and but for the larger size resembles it rather closely in the nut and style. It differs, however, in the coarser habit, the leaf-sheaths disintegrating into fine reticulate fibres, the larger and relatively much broader spikelet, and the rather larger, more oblong, more obtuse single-nerved muticous glumes. It is also allied to the Australian *F. simplex* S. T. Blake, but the latter has rather prominently swollen culm-bases, sheaths splitting into straight fibres, 3–5-nerved brownish glumes, entirely glabrous rather stout style and more shining nut cuneate at its base. On the other hand *F. cardiocarpa* F. Muell. is an entirely different plant, differing in almost every respect except for the solitary spikelet and three stigmas.

Fimbristylis pauciflora R. Br. Prodr. 225. 1810; Kükenth. Mitteil. Thüring. Bot. Ver. N. F. **50**: 9. 1943.

Fimbristylis filiformis (Nees) Kunth, Enum. **2**: 221. 1837.
Scirpus pauciflorus (R. Br.) Poir. Encycl. Suppl. 98. 1817.
Trichelostylis filiformis Nees in Wight, Contrib. 102. 1834.

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7531*, August 1936, savannahs, abundant on hard-pans and swamp margins; Gaima, Lower Fly R. (east bank), *Brass 8357*, Nov. 1936, covering patches of sour soil in savannah-forest (det. Uittien); Wuroi, Oriomo R., *Brass 5817*, Jan.–March 1934, alt. 10 m., plentiful, shaded ground on a clearing in savannah, flat spreading and rather fleshy.

Brass 7531 was recorded by Kükenthal, l.c., as new for New Guinea; previously known from northern and north-eastern Australia, other parts of Malaysia, and southern and eastern Asia.

Brass 5817 represents what appears to be the usual state in which three stigmas are present. In *Brass 7531* some flowers have two stigmas only, and flowers with two stigmas are the rule in *Brass 8357*. Nuts produced from flowers with three stigmas are always finely 3-ribbed and ± trigonous, though at times distinctly compressed. Three-ribbed nuts have also been observed produced from flowers with two stigmas, though biconvex two-ribbed nuts are more usual. Both trigynous and digynous flowers have been observed on a collection from Johore, *Ngadiman in Singapore Field No. 36784*.

Fimbristylis pumila Benth. Lond. Jour. Bot. **2**: 239. 1843, from Amboina, was later referred by its author in Fl. Austral. **7**: 303. 1878, and by C. B. Clarke in Hook. f. Fl. Brit. Ind. **6**: 633. 1893, to *F. pauciflora*. It was described as having a glabrous style with two stigmas and one-nerved oblong glumes, features which do not well accord with *F. pauciflora*.

Of the latter I have examined twelve good sets of specimens ranging from south-east Queensland to the Malay Peninsula, and in all these I find the style minutely ciliate and the glumes three- to seven-nerved and as much ovate as oblong. Bentham may have overlooked the minute sparse ciliation of the style, while the lateral nerves are often close to the keel of the glume.

Fimbristylis pauciflora is rather easily recognised by its small, unusually narrow, relatively few-flowered spikelets.

As a general rule in *Fimbristylis*, the number of stigmas is very constant in each species. *Fimbristylis pauciflora* shares with *F. tetragona* R. Br. the peculiarity of having either two or three stigmas. In *F. cymosa* R. Br., three stigmas occur in the lower part of the spikelet, but in the upper flowers there are often only two.

Fimbristylis recta F. M. Bail. 3rd Suppl. Syn. Queensl. Fl. 80. 1890; S. T. Blake, Proc. Roy. Soc. Queensl. **58**: 44. 1947.

Fimbristylis xyridis R. Br. var. *rigidula* Benth. Fl. Austral. **7**: 307. 1878.
Fimbristylis stricticulmis Domin in Biblioth. Bot. **20** (85): 452. 1915.

PAPUA: Western Division: Tarara, Wassi Kussa R., *Brass 8714*, Jan. 1937, savannah-forests, common in grass on ridges.

A distinctive species known previously only from northern Australia and Hammond Island in Torres Strait. It was discussed in some detail by S. T. Blake, l.c.

Sect. **Eufimbristylis** Boeck.

Fimbristylis ferruginea (L.) Vahl, Enum. **2**: 291. 1806; K. Schum. Notizbl. Bot. Gart. Mus. Berlin **2**: 98. 1898; in Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee 197. 1901; Valck. Suring. Nova Guin. Bot. **8**: 702. 1912; Kükenth. Bot. Jahrb. **59**: 48. 1924, **69**: 258. 1938.

Fimbristylis brevifolia R. Br. Prodr. 228. 1810.
Scirpus ferrugineus L. Sp. Pl. 74. 1753.
Scirpus brevifolius (R. Br.) Poir. Encycl. Suppl. **5**: 99. 1817.

PAPUA: Western Division: Gaima, Lower Fly R. (east bank), *Brass 8308*, Nov. 1936, common on open sandy foreshores; Gaima, Lower Fly R. (east bank), *Brass 8313*, Nov. 1936, common on sandy foreshores; Upper Wassi Kussa R. (left branch), *Brass 8642*, Jan. 1937, abundant in brackish swamp; Daru Island, *Brass 6212*, Feb. 1936, gregarious in limited pure stands, associated with *Zoysia pungens* on saline marshy ground; Daru Island, *Brass 6286*, March 1936, scattered in marginal shallows of large swamp. Central District: Kerema, *Brass 1224*, March 1926, on banks of tidal creeks; Arva R., *Carr 11436*, Feb. 1935, sea-level, marshy places near beach, about 18 in. tall (CANB; very young!).

Brass 1224 and *Carr 11436* are cited by Kükenthal, 1938, l.c.; *Brass 8313* was received as having been determined by Kükenthal as *F. ferruginea* Vahl var. *tristachya* (R. Br.) Domin. It represents a not uncommon state of the species with the inflorescence reduced to one or two spikelets, commonly seen on young or small plants. It seems pointless to

give such reduced states taxonomic status. I doubt very much whether it truly represents *F. tristachya* R. Br., and in any case, if this be regarded as a variety of *F. ferruginea*, the legitimate ternary combination would be *F. ferruginea* (L.) Vahl var. *foliata* Benth. Fl. Austral. 7: 312. 1878, the epithet *foliata* having priority in the required position. The other specimens were received as having been determined by Uittien. The species is widely spread in the warmer parts of the world.

Fimbristylis marianna Gaud. in Freyc. Voy. 413. 1826.

Fimbristylis maxima K. Schum. in Hollr. Fl. Kaiser Wilhelmsl. 24. 1889, in Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee 196. 1901; Valck. Suring. Nova. Guin. Bot. 8: 702. 1912; **syn. nov.**

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7847, 7878*, Sept. 1936, common on wet grass plains (both det. Kükenthal); Wuroi, Oriomo R., *Brass 5734*, Jan.–March 1934, alt. 10–30 m., common all through savannahs.

NORTH-EAST NEW GUINEA: Augusta R., *Hollrung 836*, in 1877 (MEL; duplicate TYPE of *F. maxima*).

New for Papua; elsewhere known from North-East New Guinea, Marianne Islands and Philippine Islands. I have relied on Kükenthal's determination of *Brass 7847* and *7878* for my concept of the species and the consequent reduction of *F. maxima* to synonymy.

Fimbristylis aestivalis (Retz.) Vahl, Enum. 2: 288. 1806.

Fimbristylis aestivalis (Retz.) Vahl f. *glabra* Kükenth. Bot. Jahrb. **59**: 49. 1924; **syn. nov.**

Scirpus aestivalis Retz. Obs. **4**: 12. 1786.

PAPUA: Western Division: Penzara, between Morehead and Wassi Kussa Rivers, *Brass 8438*, Dec. 1936, wet shaded banks of a permanent waterhole (det. Kükenthal).

Brass's plant, representing the usual pubescent state, forms the first record of the species for Papua. Kükenthal, l.c., records as f. *glabra* a glabrous form from North-East New Guinea. Elsewhere the species is known from Australia to southern and south-eastern Asia.

Fimbristylis annua (All.) R. & S. Syst. 2: 95. 1817.

Scirpus annuus All. Fl. Pedem. 2: 227. 1785.

PAPUA: Western Division: Wuroi, Oriomo R., *Brass 6069*, Jan.–March 1934, alt. 30 m., uncommon tufted species on savannah; Daru Island. *Brass 6248*, March 1936, common on damp soil in savannah-forest (det. Kükenthal as *F. diphylla* [Retz.] Vahl f. *tomentosa* [Vahl] Kükenth.); Daru Island, *Brass 6369*, March 1936, plentiful in drainage ditches in savannah-forest. Central Division: Baroka, Nakeo District, *Brass 3732*, April 1933. alt. 30 m., common, damp savannah flats, plant grayish.

For discussion, see under *F. dichotoma*.

Fimbristylis dichotoma (L.) Vahl, Enum. **2**: 287. 1806.

Fimbristylis diphylla (Retz.) Vahl, Enum. **2**: 289. 1806; K. Schum. in Warb. Bot. Jahrb. **13**: 265. 1891, Notizbl. Bot. Gart. Mus. Berlin **1**: 47. 1895, **2**: 97. 1898, in Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee 196. 1901; Valck. Suring. Nova Guin. Bot. **8**: 702. 1912; Ridl. Trans. Linn. Soc. II. Bot. **9**: 242. 1916.

Fimbristylis polymorpha Boeck. Linnaea **37**: 14. 1871, in Engl. Forschungsr. S. M. S. Gazelle **4** (1): 17. 1889.

Fimbristylis novae-brittaniae Boeck. Bot. Jahrb. **5**: 93. 1884, in Engl. Forschungsr. S. M. S. Gazelle **4** (1): 11. 1889; K. Schum. Bot. Jahrb. **9**: 195. 1888, Notizbl. Bot. Gart. Mus. Berlin **2**: 97. 1898, in Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee 196. 1901; Valck. Suring. Nova Guin. Bot. **8**: 703. 1912.

Fimbristylis annua (All.) R. & S. var. *diphylla* (Retz.) Kükenth. Bot. Jahrb. **59**: 47. 1924, *nomen* ex C. E. C. Fischer, Fl. Pr. Madras 1658. 1931.

NETHERLANDS NEW GUINEA: Balim R., *Brass 11731*, Dec. 1938, alt. 1600 m., common on grassy deforested slopes (leaves conspicuously hairy!); Balim R., *Brass 11816*, Dec. 1938, alt. 1600 m., common on sandy, long-deforested slopes, erect tufts 60–80 cm. high (leaves hairy!); Bele R., 18 km. NE. of Lake Habbema, *Brass 11489*, Nov. 1938, alt. 2200 m., common on grassy, formerly cultivated slopes, small clumps 60–80 cm. high (leaves glabrous!).

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7927*, Sept. 1936, savannah, abundant on seepage area (plant almost entirely glabrous!; det. Uittien as *F. annua* [All.] R. & S.); Lake Daviumbu, Middle Fly R., *Brass 7521*, August 1936, savannah hard-pans (almost entirely glabrous!; det. Uittien as *F. annua* [All.] R. & S.); Gaima, Lower Fly R. (east bank) *Brass 8265*, Nov. 1936, open savannah-forest, plentiful in firm-set soil, inflorescence dark brown (leaves slightly hairy!; det. Uittien as *F. annua* [All.] R. & S.); Gaima, Lower Fly R. (east bank), *Brass 8307*, Nov. 1936, plentiful on open sandy foreshores (almost glabrous!; det. Uittien as *F. annua* [All.] R. & S.). Central Division: Kanosia, *Carr 11034*, Jan. 1935, sea-level, open places under light shade (glabrous!); Huia, *Brass 524*, October 1925, coast sand hills (nearly glabrous!); Baroka, Nakeo District, *Brass 3729*, April 1933, alt. 30 m., common, damp savannah flats (nearly glabrous!); Mafulu, *Brass 5480*, Sept.–Nov. 1933, alt. 1250 m., common on roadside (leaves ± hairy!); Mafulu, *Brass 5328*, Sept.–Nov. 1933, alt. 1250 m., grassy seepages on roadside, uncommon, plant bluish green, inflorescence erect (leaves distinctly hairy!); Mafulu, *C. T. White 600*, July–August 1918, alt. ca. 1200 m. (leaves distinctly hairy!).

Fimbristylis annua (All.) R. & S., *F. diphylla* (Retz.) Vahl and allied forms have been a fertile source of difficulty since the time of Linnaeus. According to C. B. Clarke in Thistleton-Dyer, Fl. Trop. Afr. **8**: 416. 1902, "some closely allied plants, esteemed mere forms of *F. diphylla* by Kunth and Boeckler, are here regarded as distinct; even thus narrowed down, our *F. diphylla* has 140 names. It should, moreover, be understood that *F. diphylla* is so close to the preceding *F. dichotoma* that different cyperologists sort the material, as between these two, differently." On the pre-

ceding page Clarke cites *Scirpus annuus* All. (which is *Fimbristylis annua* [All.] R. & S.) as a synonym.

According to C. E. C. Fischer, Kew Bull. **1935**: 149–50. 1935, the type of *Scirpus diphyllus* Retz. and consequently of *Fimbristylis diphylla* (Retz.) Vahl is identical with the type of *Scirpus dichotomus* L., so that the plant which has been called *F. diphylla* (Retz.) Vahl must be called ***F. dichotoma*** (L.) Vahl. Another name thus has to be applied to the plant which has been passing under the name of *F. dichotoma* (L.) Vahl, and according to Fischer, l.c., p. 149, the legitimate combination is *Fimbristylis bisumbellata* (Forsk.) Bubani.*

To my mind, *F. annua* (All.) R. & S. is conspecific with *F. depauperata* R. Br., and I have suggested previously, Univ. Queensl. Papers Dept. Biol. 1(13): 3. 1940, that this is specifically distinct from *F. dichotoma* (*F. diphylla*), differing in the constantly annual habit, the softer and softly hairy leaves and bracts, the more or less hairy culms and rays, the glumes often minutely ciliolate at the upper edge, the cells composing the glumes less distinctly oblong (more nearly square) in shape, and in the relatively shorter and broader style. *Fimbristylis dichotoma* has sometimes hairy leaf-blades and more rarely hairy culms, but the hairs are more rigid and the blades stiffer than in *F. annua*. In this restricted sense, *F. annua* seems to have been previously unknown from New Guinea.

Fimbristylis dichotoma, or allied forms, has been reported under other names from New Guinea, apart from those recorded in the synonymy above. Of some of these I am uncertain of the taxonomic status, and some seem to be invalid names.

Fimbristylis dipsacea (Rottb.) C. B. Clarke in Hook. f. Fl. Brit. Ind. 6: 635. 1895.

Scirpus dipsaceus Rottb. Descr. et Ic. 56, *t. 12, fig. 1*. 1773; F. Muell. Pap. Pl. **2**: 35. 1886.
Echinolytrum dipsaceum (Rottb.) Desv. Jour. Bot. **1**: 21, *t. 1*. 1808.
Isolepis dipsacea (Rottb.) R. & S. Syst. **2**: 119. 1811.

PAPUA: Western Division: Strickland R., *Bäuerlen* in 1885 (BRI, MEL).

This collection, the only one recorded for New Guinea, was recorded by Mueller, l.c., as *Scirpus dipsaceus*. The formal transfer of the species to *Fimbristylis* was made by C. B. Clarke, l.c., though this author there cited Benth. in Gen. Pl. 3: 1049. Bentham gave reasons why it should be placed under *Fimbristylis*, but did not make the transfer.

Sect. **Trichelostylis** (Lestib.) A. Gray

Fimbristylis signatus nom. nov.

* From Fischer's data, it is doubtful if this combination was validly published by Bubani; I have not seen the publication.

Fimbristylis debilis F. Muell. Fragm. Phyt. Austr. **1:** 198. 1859, non Steud. Syn. Cyper. 109. 1855.
Iriha debilis (F. Muell.) O. Ktze. Rev. Gen. Pl. **2:** 753. 1891.

PAPUA: Western Division: Daru Island, *Brass 6250*, March 1936, frequent on damp soil in savannah-forest.

New for New Guinea; previously known only from northern Australia.

Fimbristylis eragrostis (Nees & Meyen) Hance, Jour. Linn. Soc. Lond. **13**: 132. 1873; Kükenth. Mitteil. Thüring. Bot. Ver. N. F. **50**: 9. 1943.

Abildgaardia eragrostis Nees & Meyen in Wight, Contrib. 95. 1834.

PAPUA: Western Division: Tarara, Wassi Kussa R., *Brass 8405*, Dec. 1936, savannah-forest, common on sour gray soil; Wuroi, Oriomo R., *Brass 5706*, Jan.–March 1934, alt. 10–30 m., common on lower savannah ridges. Central Division: Astrolabe Range, *W. E. Armit* in 1894–5 (MEL). South-Eastern Division: Sud-est Island, *W. MacGregor* in 1889 (MEL).

Brass 8405 was cited by Kükenthal, l.c., as new for New Guinea. The species extends northwards to China and southwards to Queensland.

Fimbristylis globulosa (Retz.) Kunth, Enum. **2**: 231. 1837; Kükenth. Bot. Jahrb. **59**: 49. 1924, **69**: 258. 1938; Ohwi, Bot. Mag. Tokyo **56**: 202. 1942.

Scirpus globulosus Retz. Obs. **6:** 19. 1791.

NETHERLANDS NEW GUINEA: Bernhard Camp, Idenburg R., *Brass 14087*, April 1939, alt. 50 m., on thick beds of floating grass (*Leersia*) in a lagoon, erect in large clumps about 1.2 m. high.

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7604*, August 1936, occasional on floating islands of swamps and lagoons.

New for Papua. Previously known from Netherlands New Guinea (Ohwi, l.c.), North-East New Guinea, New Ireland, Micronesia, Philippine Islands, Malaya and India.

Fimbristylis insignis Thw. Enum. Pl. Zeyl. 349. 1864.

PAPUA: Western Division: Mai Kussa R., *W. MacGregor* in 1890 (MEL).

New for New Guinea. Originally described from Ceylon and since reported from China, Borneo and Queensland. MacGregor's specimen was written up by F. Mueller simply as "Fimbristylis."

Fimbristylis complanata (Retz.) Link, Hort. Berol. **1**: 292. 1827; Valck. Suring. Nova Guin. Bot. **8**: 703. 1912; Palla in Rechinger, Denkschr. Math.-Naturw. Kais. Akad. Wiss. Wien **89**: 498. 1913.

Scirpus complanatus Retz. Obs. **5:** 14. 1789.

Fimbristylis autumnalis (L.) R. & S. var. *complanata* (Retz.) Kükenth. Bot. Jahrb. **59:** 50. 1924.

PAPUA: Central Division: Port Moresby, *C. T. White 4*, July–August 1918.

New for Papua, but known from most of the warmer parts of the Old World. It is probably this species which was recorded as *Fimbristylis autumnalis* (L.) R. & S. by Warburg, Engl. Bot. Jahrb. **18**: 186. 1893 and by K. Schumann and Lauterbach, Fl. Deutsch. Schutzgeb. Südsee 196. 1901.

Fimbristylis microcarya F. Muell. Fragm. Phyt. Austr. 1: 200. 1859.

Fimbristylis autumnalis (L.) R. & S. var. *microcarya* (F. Muell.) Kükenth. Bot. Jahrb. **69:** 258. 1938.

PAPUA: Central Division: Port Moresby, *Carr 11847*, April 1935, open savannah land by the sea (CANB).

This collection was cited by Kükenthal, l.c., as *F. autumnalis* (L.) R. & S. var. *microcarya* (F. Muell.) Kükenth., comb. nov. It is the only specimen I have seen from outside Australia, though according to C. B. Clarke in Hook. f. Fl. Brit. Ind. **6**: 646. 1893 (where it is treated as a variety of *F. complanata* [Retz.] Link) the species extends to India. My reasons for regarding *F. microcarya*, *F. complanata*, and *F. autumnalis* as distinct species are given in Proc. Roy. Soc. Queensl. **48**: 93. 1937.

Fimbristylis salbundia Kunth, Enum. **2**: 230. 1837.

PAPUA: Central Division: Urunu, Vanapa Valley, *Brass 4805*, July–August 1933, alt. 1900 m., common species in small swamps on grass country.

New for New Guinea; known previously from Assam and Burma. C. B. Clarke in Hook. f. Fl. Brit. Ind. **6**: 647. 1893 and ex Domin, Biblioth. Bot. **85**: 463. 1915, recorded it from Australia. Domin quoted a collection from the Victoria R., *F. Mueller*, but the specimens belong to *F. trachycarya* F. Muell., a species discussed by me in Proc. Roy. Soc. Queensl. **48**: 92. 1937. Brass's specimen agrees with pieces of *Wallich 3526* ex herb. Berlin and ex herb. Kew, cited in the original description and by C. B. Clarke, l.c.

Fimbristylis miliacea (L.) Vahl, Enum. **2**: 287. 1806, quoad basonym.

Scirpus miliaceus L. Syst. Veg. **10:** 868. 1759.
Isolepis miliacea (L.) Presl. Rel. Haenk. **1:** 188. 1830.
Trichelostylis miliacea (L.) Nees in Wight, Contrib. 103. 1834, quoad basonym.
Iriha miliacea (L.) O. Ktze. Rev. Gen. Pl. **2:** 752. 1891.
Scirpus bengalensis Pers. Syn. **1:** 68. 1805.
Fimbristylis ? bengalensis (Pers.) R. & S. Syst. **2:** 94. 1817.
Scirpus quinquangularis Vahl, Enum. **2:** 279. 1806; **syn. nov.**
Trichelostylis quinquangularis (Vahl) Nees in Wight, Contrib. 104. 1834; **syn. nov.**

Fimbristylis quinquangularis (Vahl) Kunth, Enum. **2:** 229. 1837; **syn. nov.**
Iriha quinquangularis (Vahl) O. Ktze. Rev. Gen. Pl. **2:** 752. 1891; **syn. nov.**
Scirpus pentagonus Roxb. Fl. Ind. **1:** 229. 1820; ed. Carey **1:** 218 (1831); **syn. nov.**
Isolepis ? pentagona R. & S. Syst. Mant. **2:** 69. 1824; **syn. nov.**
Fimbristylis boeckeleri Steud. Syn. Cyp. 113. 1855; **syn. nov.**

PAPUA: Central Division: Baroka, *Brass 3733*, April 1933, alt. 30 m., common on damp savannah flats, plant pale green.

A widely spread species not previously recorded for New Guinea. The application of the name is explained under the following species.

Fimbristylis littoralis Gaud. in Freyc. Voy. Bot. 413. 1826.

Scirpus tetragonus Poir. Encycl. **6:** 767. 1804, nec (R. Br.) Poir. Encycl. Suppl. **5:** 98. 1817, nec *Fimbristylis tetragona* R. Br. 1810.
Scirpus tetragonus Roxb. Fl. Ind. **1:** 232. 1820; ed. Carey **1:** 228. 1832.
Isolepis ? tetragona R. & S. Syst. Mant. **2:** 69. 1824.
Fimbristylis tetragona A. Dietr. Sp. Pl. **2:** 152. 1833, non R. Br. 1810.
Fimbristylis flaccidula Zoll. Syst. Verz. Ind. Archip. **2:** 61. 1854.
Fimbristylis flaccida Steud. Syn. Cyp. 113. 1855.
Fimbristylis quadrangularis A. Dietr. ex Steud. Syn. Cyp. 114. 1855.

NETHERLANDS NEW GUINEA: Bernhard Camp, Idenburg R., *Brass 13780*, April 1939, frequent on logs floating in lagoons and backwaters at 50 m. alt.

PAPUA: Western Division: Palmer R., 1 mi. above junction with Black R., *Brass 6946*, June 1936, abundant on silt-covered gravel banks; Strickland R., *W. Bäuerlen 22*, July 1885 (BRI, MEL); Strickland R., *W. Bäuerlen 529*, Nov. 1885, on river banks (MEL); Gaima, Lower Fly R. (east bank), *Brass 8310*, Nov. 1936, common on open sandy foreshores; Daru Island, *Brass 6042*, March 1934, very common on swampy savannahs. Central Division: Thu, Vaitata R., *Brass 1016*, Feb. 1926, in the sago swamps; Laloki R., *C. T. White 173*, July–August 1918.

This is the widely spread plant commonly called *Fimbristylis miliacea* (L.) Vahl; *Brass 6946, 8310* had been so determined by Uittien, and the species has been recorded for New Guinea under this name by F. Muell. Pap. Pl. **2:** 35. 1886; K. Schum. Notizbl. Bot. Gart. Mus. Berlin **2:** 98. 1898, in Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee 197. 1901; Valck. Suring. Nova Guin. Bot. **8:** 703. 1912; and Kükenth. Bot. Jahrb. **59:** 50. 1924; also *F. miliacea* forma *tenerrima* Valck. Suring., l.c., Kükenth., l.c.

C. B. Clarke, Jour. Linn. Soc. Lond. **30:** 312. 1894, stated that the type of *Scirpus miliaceus* L. is a plant of *Fimbristylis quinquangularis* (Vahl) Kunth. Through the kindness of Dr. E. D. Merrill and Dr. L. M. Perry, I have seen a small photograph of the Linnaean type, but unfortunately the photograph is not sufficiently sharp for critical comparison with specimens. Through the courtesy of the Director of the Royal Botanic Gardens, Kew, Mr. E. Nelmes kindly compared some Australian specimens with the Linnaean type. Mr. Nelmes reported as follows:

I have examined the "type" specimen of *Scirpus miliaceus* in the Linnaean herbarium and agree with C. B. Clarke that it represents the species generally known as *Fimbristylis quinquangularis* (Vahl) Kunth. It is a good match of Mr. S. T. Blake's specimen, no. 11319.

Linnaeus has written "miliaceus" on the sheet, and I think the specimen may be accepted as his type. There is, however, another Linnaean specimen, placed next after the type, which has some bearing on this matter, because it is the species which has always been known as *Scirpus miliaceus* L., agreeing well with Mr. Blake's nos. 7818, 8195, and 8784. C. B. Clarke . . . . does not mention this second sheet, probably because it bears no inscription by Linneaus. . . .

The combination *Fimbristylis miliacea* based on Linnaeus' name must be restricted to the species represented by Linnaeus' type, i.e., to the plant commonly called *F. quinquangularis*; no other course can be taken that would be in accord with the International Rules of Nomenclature. C. B. Clarke's suggestion, l.c., that Linnaeus would surely have esteemed the two as one species, does not warrant the deliberate continuance of the misapplication of the name. N. L. Burman, Fl. Ind. *22, t. 9, fig. 2.* 1768, seems to have been the first to misapply Linnaeus' name, and since then the misapplication has been scarcely questioned.

Several names have been applied to one or other of the two species commonly known as *F. miliacea* and *F. quinquangularis*. Of these only *Scirpus miliaceus* L., *Scirpus bengalensis* Pers., *Scirpus quinquangularis* Vahl, *Scirpus pentagonus* Roxb., *Fimbristylis boeckeleri* Steud., *Fimbristylis flaccida* Steud., and *Fimbristylis flaccidula* Zoll. were based on specimens, and they are the basonyms of the remaining names. I have seen types of a portion thereof of *S. bengalensis* (L), *S. quinquangularis* (C), *F. littoralis* (P) and *F. flaccida* (P). *Fimbristylis flaccida* and *F. flaccidula* were probably based on the same collection, but I have not been able to verify this. *Scirpus tetragonus* Poir. and *S. tetragonus* Roxb. were described quite independently of each other; from the descriptions and specimens from the type-localities there seems no doubt as to the interpretations of these names or of *F. boeckeleri.* I am not so sure of *S. pentagonus*, though the description applies well enough to the leafless states of the species commonly called *Fimbristylis quinquangularis. Blake 11319*, matched with the type of *S. miliaceus*, also matches the type of *S. quinquangularis.*

Another name must be found for the species commonly called *Fimbristylis miliacea.* The earliest epithet in the required position is in the combination *Scirpus tetragonus* Poir. Encycl. 6: 767. 1804, but this is not available under *Fimbristylis* because of *F. tetragona* R. Br. and upon which Poiret's later homonym was based in 1817. The next is in *Fimbristylis littoralis* Gaud., and this appears to be the correct name for the species. *Scirpus bengalensis* Pers. has been generally referred to this species, but Persoon's description ("involucro tetraphyllo spiculis. . . . ovatis (minutis): squamis concavo-carinatis mucronatis") agrees better

with true *Fimbristylis miliacea*; a recent examination of the type (L) confirms this.

Two other names require mention. "*Fimbristylis angularis* Steud." Syn. Cyp. 116. 1855 has been referred to *F. miliacea* (*F. quinquangularis*) by some. Steudel's combination was based on *Isolepis angularis* Schrad. ex R. & S. Syst. Mant. 2: 69. 1824, which appears to have been based on *Fimbristylis angularis* Link, Enum. Hort. Berol. 1: 289. 1821, so that Steudel's transfer was quite unnecessary. Boeckeler's description (Linnaea **37**: 30–31. 1871) of what appears to be Link's type refers to some other species, particularly as to the long bracts, relatively large spikelets and sometimes bifid styles. *Fimbristylis trachycarya* F. Muell. Fragm. 1: 199. 1859, sometimes referred to *F. littoralis*, belongs to an endemic Australian species which has been discussed elsewhere (S. T. Blake, Proc. Roy. Soc. Queensl. **48**: 92. 1937).

Fimbristylis littoralis and *F. miliacea* do not differ greatly in spikelet structure, though the more or less globular, very obtuse, scarcely at all angular spikelets of the former with their muticous and more or less concave glumes are, with a little experience, readily enough distinguished from the ovoid, less obtuse, more distinctly angular spikelets of the latter with their rather prominently keeled, more or less distinctly apiculate glumes. The foliage of the two species is markedly dissimilar, but is sometimes poorly developed. The leaves of *F. littoralis* are vertically flattened, finely striate without prominent veins, with rather thin edges, and are usually borne as distichous, more or less flabellate tufts between the culms. The leaves of *F. miliacea* are of the usual *Fimbristylis* type, dorso-ventrally flattened with a prominent midrib and rib-like margins. The revised synonymy of the two species is given above.

Fimbristylis furva R. Br. Prodr. 228. 1810.

PAPUA: Western Division: Mai Kussa R., *W. MacGregor* in 1890 (MEL).

Previously known only from Queensland, including islands in Torres Strait.

Fimbristylis pycnocephala Hillebr. Fl. Haw. Isl. 473. 1888.

Fimbristylis cymosa R. Br. var. *capitato-umbellata* Hillebr. Fl. Haw. Isl. 473. 1888; **syn. nov.**

Fimbristylis cymosa R. Br. var. *subcapitata* C. B. Clarke ex Hemsl. Jour. Linn. Soc. Lond. **30**: 197. 1894.

Fimbristylis cymosa R. Br. var. *pycnocephala* (Hillebr.) Kükenth. in Cristophersen, Bull. Bishop Mus. **128**: 20. 1935.

SOLOMON ISLANDS: Ulawa, *Brass 2990*, October 1932, ocean foreshore, common.

New for the Solomon Islands; previously known from the Hawaiian Islands (!), Tonga (!), New Caledonia and Samoa.

In this species, the spikelets may all be aggregated in a single dense head or clustered on the rays of an umbel-like inflorescence; all intermediate states occur. Hawaiian plants with the looser inflorescences were referred by Hillebrand to *F. cymosa* R. Br. and *F. cymosa* var. *capitato-umbellata*, but all states of *F. pycnocephala* may be distinguished from the Australian *F. cymosa* as follows:

Spikelets ± oblong; broad, hyaline margins of glumes loosely reticulate; nut somewhat shining, smooth or minutely striate only, the epidermal cells minute, square or nearly so, arranged in fairly regular vertical series but the transverse arrangement ± irregular ..... *F. pycnocephala.*

Spikelets ovoid; broad, hyaline margins of glumes not evidently reticulate, the cells composing them very small with inconspicuous margins; nut somewhat roughened, rather indistinctly striate vertically and horizontally, the minute epidermal cells transversely narrowly oblong, arranged regularly in both vertical and horizontal series ..... *F. cymosa.*

Sect. **Abildgaardia** (Vahl) Benth.

Fimbristylis cinnamometorum (Vahl) Kunth, Enum. 2: 229. 1837; Kükenth. Mitteil. Thüring. Bot. Ver. N. F. **50**: 9. 1943.

Scirpus cinnamometorum Vahl, Enum. 2: 278. 1806.
Fimbristylis cyperoides R. Br. Prodr. 228. 1810.

PAPUA: Western Division: Tarara, Wassi Kussa R., *Brass 8408*, Dec. 1936, savannah-forest, abundant on wet flats; Lake Daviumbu, Middle Fly R., *Brass 7876*, Sept. 1936, occasional in small erect tufts on wet grass plains; Gaima, Lower Fly R. (east bank), *Brass 8262*, Nov. 1936, plentiful on hard soil in open savannah-forests.

These are the only collections known from New Guinea, though the species is known to range from NE. Australia to Ceylon and SE. Asia.

Fimbristylis cinnamometorum and *F. cyperoides* have sometimes been treated as distinct species on the grounds that the former (from Ceylon, Pegu and China) is an annual, while the latter (from Australia to the Philippine and Caroline Islands) has a prominent rhizome. But the type of *Scirpus cinnamometorum* (C) is from a perennial plant and is well matched by many Australian specimens; the degree of development of a rhizome depends on the age of the plant and varies greatly in herbarium material.

Fimbristylis stenochlaena Kükenth. Mitteil. Thüring. Bot. Ver. N. F. **50**: 11. 1943.

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7840*, Sept. 1936, very abundant on wet grass plains, leaves of young plants arranged spirally in a flat rosette (TYPE collection).

The plants seen by me appear to be somewhat larger than those seen by Kükenthal, 30–50 cm. high, with asperulous many-ribbed rather than smooth obsoletely pentagonal sulcate culms, with 9 or 10 (not 4–6)

-rayed inflorescences with rather longer and broader mature spikelets 9–11 mm. long and 2–3 mm. wide (described by Kükenthal as 8–9 mm. long and 1.5–2 mm. wide). I find the glumes acute and more or less cuspidulate rather than long acuminate, and the nuts (five examined) obovoid, not at all pyriform, 0.8 mm. long, 0.55 mm. wide.

Fimbristylis fusca (Nees) C. B. Clarke in Hook. f. Fl. Brit. Ind. 6: 649. 1893.

Abildgaardia fusca Nees in Wight, Contrib. Bot. Ind. 95. 1834.

NETHERLANDS NEW GUINEA: Balim R., *Brass 11744*, Dec. 1938, alt. 1600 m., common among the grass on long-deforested slopes.

New for New Guinea; previously known from India and the Philippine Islands to Java and the Moluccas. The plants are glabrous.

Clarke, l.c., cites "Benth. in Gen. Pl. iii. 1048" as the author of the combination, but Bentham here merely reduces the genus *Abildgaardia* to a section of *Fimbristylis*. In Index Kewensis, Suppl. 4: 92. 1913 the author of the combination is given as "*Benth. ex C. B. Clarke in Hook. f. Fl. Brit. Ind.* vi. 649 (1893)."

Fimbristylis fimbristyloides (F. Muell.) Druce, Rep. Bot. Exch. Club Brit. Isles 1916: 623. 1917.

Abildgaardia fimbristyloides F. Muell. Fragm. Phyt. Austr. 8: 273. 1874.

PAPUA: Central Division: Rona, Laloki R., *Brass 3576*, April 1933, alt. 450 m., common, wet places on open grassy hillsides.

New for New Guinea; previously known only from northern Queensland.

Fimbristylis intonsa sp. nova (Sect. *Abildgaardia*). Fig. 2.

Herba annua, usque ad 16 cm. alta. Culmi fasciculati, setacei, stricti, erecti, quinquangulares angulis angustis elevatis sursum scabris. Folia pauca, usque ad 5 cm. longa, culmi tertiam partem raro adaequantia, 1–2 mm. lata, caulina 1–2; vaginae striatae, antice hyalinae, summa prope orificem pubescens, ceterae glabrae; laminae lineares, sursum admodum angustatae, apice obtusae vel acutae, falcatae vel tortuosae, planae vel incurvae, coriaceae, haud carinatae, paucinerves, marginibus leviter incrassatae sursum scabrae, supra prominule subtus indistincte cellulosoreticulatae, eae foliorum caulinorum saepe multo breviores angustioresque. Anthela simplex vel composita, 2–7-radiata, laxa. Bracteae 1–2 infimae subfoliaceae usque ad 12 mm. longae, vel omnes setaceae, saepe minimae; bracteolae minimae. Radii setacei, compressi, scabri, usque ad 2.5 cm. longi; radioli suberecti, usque ad 7 mm. longi. Spiculae oblongae, acutae, compressae, saepe tortae, 5–8 mm. longae, 1.5–1.8 mm. latae, multi- et densiflorae; rhachilla excavata alata. Glumae distichae vel sursum specie laxe spiraliter dispositae, brunneae vel ferrugineae, latissime ovatae,

obtusae, mucronatae, 1-nerves, carinatae carina curva sursum valida excurrente, fere omnino albo-pubescentes, marginibus vix hyalinis ciliatae, 1.7–1.8 mm. longae, cellulis minutissimis; 1–2 infimae vacuae minores. Stamina 3; antherae lineares, apiculatae, 0.5 mm. longae; filamenta lata. Stylus pro ratione robustus, triquetrus, basi latiuscule pyramidatus, omnino glaber, 1 mm. longus; stigmata 3, stylo breviora. Nux albida, obovoidea fere ellipsoidea, utrinque rotundata apice leviter umbonulata, minime stipitata, obtuse trigona angulis haud prominulis, lateribus convexulis, verrucosa, 0.7 mm. longa, 0.5 mm. lata, cellulis extimis hexagonis parvis indistinctis.

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7841*, Sept. 1936, very common on wet grassy plains (TYPE).

This collection was labelled "Fimbristylis disticha Boeck. (det. Kükenthal)." It is certainly allied to *F. disticha* Boeck., but to judge from the piece of the type of this species in herb. Brisbane ex herb. Berlin, it differs in the broader, more coarsely keeled, prominently mucronate and densely pubescent glumes and the broader, more ellipsoid nut not cuneate but rounded at the base, less distinctly ribbed at the angles and with hexagonal rather than oblong external cells. According to C. B. Clarke in Hook. f. Fl. Brit. Ind. 6: 651. 1893, the glumes of *F. disticha* are minutely ciliate at the margins, but I find them glabrous. Kükenthal, Bot. Jahrb. 59: 50. 1924, and 69: 258. 1938, has recorded *F. disticha* from North-East New Guinea, but I have not seen these specimens.

The species of sect. *Abildgaardia* discussed may be distinguished as follows:

Leaves setaceous, at least half as long as culm, more or less distichous; basal sheaths ± horny; glumes scabrous with reddish glands; nut (0.8–1 mm. long) with the external cells transversely oblong. . . . . *F. cinnamometorum*.

Leaves flat, at least 1 mm. wide, less than half and sometimes scarcely one quarter as long as culm, spirally arranged, often falcate; basal sheaths not horny, prominently nerved; glumes not (or in *F. fusca* very rarely) glandular, usually pubescent (except in *F. disticha*); nut (0.6–1 mm. long) with the external cells hexagonal, not or but slightly elongated transversely.

Glumes 3–5 mm. long, the upper ones somewhat spiral; style 3–4 mm. long, 3–6 times as long as the obovoid nut; perennial (? always).

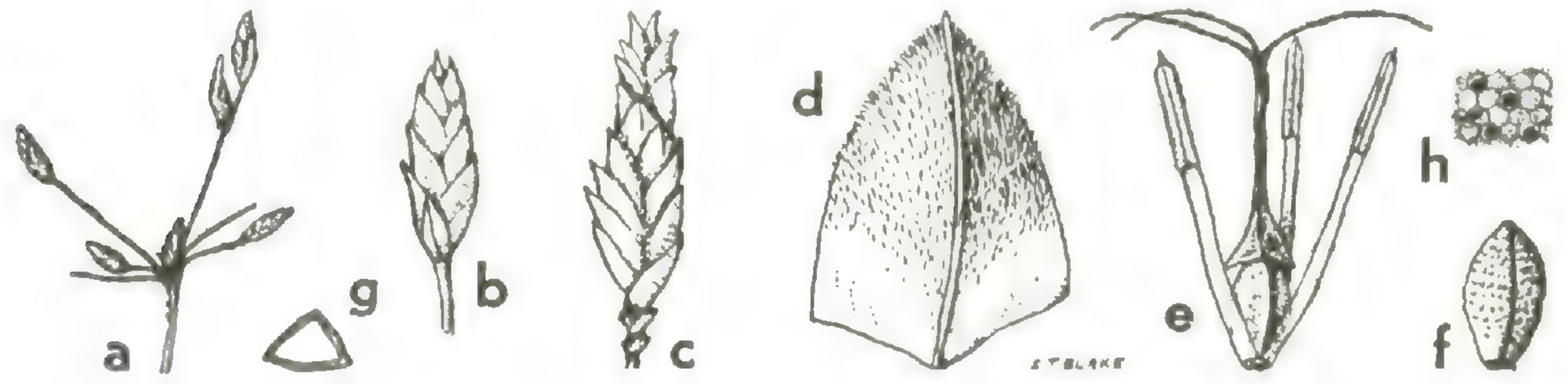

FIG. 2. *Fimbristylis intonsa* S. T. Blake: a. inflorescence, × 1; b., c. spikelets, × 3; d. glume, × 15; e. flower, × 15; f. nut, × 15; g. transverse section of nut; h. surface of nut, × 40. Figures from type.

Glumes about half as wide as long, 4–5 mm. long; style 4 mm. long; culms many-ribbed; leaves 1.5–4 mm. wide; spikelets 2–3 mm. wide. ..... *F. stenochlaena.*

Glumes more than half as wide as long, 3–4 mm. long; style about 3 mm. long; culms 5-ribbed; leaves 2 mm. wide; spikelets 1.5–2 mm. wide. ..... *F. fusca.*

Glumes up to 2.5 mm. long, regularly distichous, but the whole spikelet sometimes twisted; style 1–1.3 mm. long, less than twice as long as nut; annual plants.

Glumes glabrous, muticous or nearly so, acute, the keel slightly curved, 1.6–1.7 mm. long; nut narrowly obovate, cuneate to a very narrow base, about 0.6 × 0.35 mm. ..... *F. disticha.*

Glumes puberulous or rarely glabrous, acute, mucronulate, the keel straight or nearly so, 2–2.5 mm. long; nut broadly obovate, somewhat attenuate above the broad truncate base, about 0.75 × 0.55 mm. ..... *F. fimbristyloides.*

Glumes densely pubescent with ciliolate scarcely hyaline margins, very broad and very obtuse, rather coarsely mucronulate, the keel curved, 1.7–1.8 mm. long; nut obovate, rounded to the base, 0.7 × 0.5 mm. ..... *F. intonsa.*

Scleria Bergius

There is no recent general account of the species of *Scleria* in the Malaysian-Australian region. A revision of the Australian species was commenced some years ago and has been intensified and expanded more recently to include the Malaysian species. The following account of the Brass collections is really a preliminary revision of all the species known from New Guinea. It would seem that a large number of names for alleged new species have been based on far too scanty material, and that very little attention has been paid to individual variation. Misapplications of names have been fairly frequent; it would appear that some early botanists did not see the types of the names proposed by their predecessors (which are frequently scrappy in any case), and their often faulty identifications were blindly accepted by later botanists, possibly for want of better evidence. I have been fortunate in seeing types or isotypes of a goodly proportion of the names mentioned in this paper; of others I have seen topotypes — specimens from the type-locality which agree with the original description. Although an extensive series of specimens from Australia, Malaysia and elsewhere has now been examined, study of further material, particularly from India, may demand modifications of some of the conclusions published in this paper.

A curious fact is that there appears to be no endemic species in New Guinea. Of the thirteen accepted species, all but one (*S. polycarpa*) occur elsewhere in Malaysia and all but two or three (*S. pergracilis*, *S. motleyi* and, perhaps, *S. tessellata*) occur in Australia, some of them extending further eastward.

Scleria pergracilis (Nees) Kunth, Enum. Pl. 2: 354. 1837.

Hypoporum pergracile Nees, Edinb. New Philipp. Jour. 17: 267. 1834.

NORTH-EAST NEW GUINEA: Kani Hills near Ongoruna (Unguruna) Village, *Lane-Poole 635*, Feb. 1924 (has as strong a lemon-verbena scent as to make a whole hill-top perfumed); Partep, *Commonwealth Nutritional Survey N. S. P. 69, N. S. P. 92.*

New for New Guinea; previously known from Tropical Africa, India and Ceylon.

Scleria lithosperma (L.) Sw. Prodr. Veg. Ind. Occid. 18. 1788; Boeck. in Engl. Forschungsr. S. M. S. Gazelle 4 (1): 18. 1889; K. Schum. & Lauterb. Nachtr. Fl. Deutsch. Schutzgeb. Südsee 60. 1905; Valck. Suring. Nova Guin. Bot. 8: 711. 1902; Kükenth. Bot Jahrb. 59: 58. 1924; Ohwi, Bot. Mag. Tokyo 56: 212. 1942.

Scirpus lithospermus L. Sp. Pl. ed. 1: 51. 1753.
Schoenus lithospermus (L.) L. Sp. Pl. ed. 2: 65. 1762.
Scleria tenuis Retz. Obs. 4: 13. 1786.
Scleria capillaris R. Br. Prodr. 240. 1810.
Scleria wightiana Steud. Syn. Cyp. 176. 1855.
Hypoporum lithospermum Nees in Mart. Fl. Brasil. 2 (1): 172. 1842.
Hypoporum capillare (R. Br.) Nees, Linnaea 9: 303. 1834.

NORTH-EAST NEW GUINEA: New Britain, *Parkinson* in 1885 (MEL).

PAPUA: Western Division: Lower Fly R., east bank opposite Sturt Island, *Brass 8059*, Oct. 1936, rain-forest, tufts 60–80 cm. high, forming a scant ground cover on dry ridges; Daru Island, *Brass 6259*, March 1936, common along edge of rain-forest. Eastern Division: Lower Mori R., *Brass 1634*, June 1926, on rain-forest floor.

Cosmotropical. Further synonyms are listed by Core, Brittonia 2: 27–8. 1936. *Brass 6259, 8059* had been determined by Kükenthal.

Scleria roxburghii (C. B. Clarke) Domin, Biblioth. Bot. 85: 487. 1915.

Scleria lithosperma (L.) Sw. var. β Thw. Enum. Pl. Zeyl. 354. 1864.
Scleria lithosperma (L.) Sw. var. *roxburghii* C. B. Clarke in Hook. f. Fl. Brit. Ind. 6: 686. 1894.
Scleria lithosperma (L.) Sw. var. *linearis* Benth. Fl. Austral. 7: 430. 1878.
Scleria roxburghii (C. B. Clarke) Domin var. *australiensis* Domin, Biblioth. Bot. 85: 487. 1915; **syn. nov.**
Hypoporum roxburghii Nees ex C. B. Clarke in Hook. f. Fl. Brit. Ind. 6: 686. 1894, in syn.
Hypoporum roxburghiana Nees ex Boeck. Linnaea 38: 452. 1874, in syn.

PAPUA: Western Division: Tarara, Wassi Kussa R., *Brass 8504*, Dec. 1936, rain-forest, dense tufted ground cover 50–60 cm. high, in partial shade. Central Division: Baroka, Nakeo district, *Brass 3774*, April 1933, alt. 30 m., common in brushy rain-forest and on garden clearings; Port Moresby to Kalo, *MacGregor* in 1889 (MEL).

New for New Guinea. Known elsewhere from Queensland, Philippine Islands, India and Ceylon.

Scleria motleyi C. B. Clarke, Philipp. Jour. Sci. **2** (C): 104. 1907; Ohwi, Bot. Mag. Tokyo **56**: 213. 1942.

Scleria motleyi C. B. Clarke var. *densi-spicata* C. B. Clarke, Philipp. Jour. Sci. **2 (C)**: 104. 1907; **syn. nov.**
Scleria trigonocarpa Ridl. Jour. Str. Branch Roy. As. Soc. **46**: 228. 1906. *nomen*, Mater. Fl. Malay. Pen. (Monocot.) **3**: 110. 1907; non Steud. 1855.
Scleria trigona Merr. Philipp. Jour. Sci. **8** (C): 363. 1913.
Scleria gonocarpa Ridl. Fl. Malay Pen. **5**: 177. 1925; **syn. nov.**
Scleria sorsogonensis Elmer ex Merr. Enum. Philipp. Fl. Pl. **1**: 134. 1922, in obs., pro syn.; Elmer, Leafl. Philipp. Bot. **10**: 3541. 1938, descr. anglice.
Scleria subrostrata Elmer, Leafl. Philipp. Bot. **10**: 3542. 1938, in obs., pro syn.

NETHERLANDS NEW GUINEA: Hollandia and vicinity, *Brass 8870*, June–July 1938, alt. 100 m., rain-forest, tufted floor plant on sharp ridge crests.

Previously recorded by Ohwi, l.c., for Netherlands New Guinea; elsewhere known from Malaya, Borneo and Philippine Islands.

Scleria tessellata Willd. Sp. Pl. **4**: 315. 1805; K. Schum. in Warb. Bot. Jahrb. **13**: 267. 1891; Valck. Suring. Nova Guin. Bot. **8**: 712. 1912.

Scleria parvula Steud. Syn. Cyp. 174. 1855.
Scleria uliginosa Hochst. ex Boeck. Linnaea **38**: 471. 1874.

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7527*, August 1936, sporadic on savannahs; Lake Daviumbu, Middle Fly R., *Brass 7875*, Sept. 1936, sporadic on wet grass plains, erect in small tufts; Lake Daviumbu, Middle Fly R., *Brass 7963*, Sept. 1936, rain-forest, common in semi-shade on shores of lake.

New for Papua; known to extend in an apparently sporadic manner north and west to India and Ceylon. Some of the records of this species from Mayalsia belong to the closely allied *S. biflora* Roxb. The Australian plants referred to it by Bentham, Fl. Austral. **7**: 430. 1878 belong to other species.

Scleria novae-hollandiae Boeck. Flora **58**: 120. 1875.

Scleria merrillii Palla, Allgem. Bot. Zeitschr. **17**: Beil. 8. 1911; **syn. nov.**

PAPUA: Western Division: Wuroi, Oriomo R., *Brass 6012*, Feb.–March 1934, alt. 50 m., on a savannah ridge; Daru Island, *Brass 6427*, April 1936, gregarious on wet soil in savannah forest.

New for New Guinea; previously known from northern and northeastern Australia and the Philippine Islands.

This species was referred by Bentham, Fl. Austral. **7**: 428. 1878 to *S. laxa* R. Br., and in this he was followed by later authors. I have discussed these species as to their occurrence in Australia in Proc. Roy. Soc.

Queensl. **58**: 48–9. 1947 and **60**: 52–3. 1949. I have now seen the type and an isotype of *S. novae-hollandiae*, a photograph and a fragment of the type of *S. laxa* and isotypes of *S. merrillii*. The species is well distinguished from other small annual species by the dull white, nearly smooth surface of the more or less oblong nut and the small thin tightly appressed disc with broadly rounded lobes and shallow sinuses. The chalky appearance of most nuts is very distinctive. Kükenthal determined *Brass 6427* as *S. tessellata*, which has an ellipsoid, shining, prominently tessellated nut and a larger, thicker, more deeply divided disc with rather acute lobes and sinuses. To judge from his remarks on the disc, the specimen upon which Kükenthal based his record for New Guinea of *S. brownii* Kunth, Bot. Jahrb. **70**: 464. 1940 may also belong here.

Scleria rugosa R. Br. Prodr. 240. 1810.

Scleria lateriflora Boeck. Linnaea **38**: 455. 1874; **syn. nov.**
Scleria pubigera Makino, Bot. Mag. Tokyo **27**: 55. 1913; **syn. nov.**

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7532 A*, August 1936, savannahs, gregarious in flat tufts on hard-pans and swampy margins; Wuroi, Oriomo R., *Brass 5868*, Jan.–March 1934, alt. 30 m., rare, gray soil on low savannah ridge; Wuroi, Oriomo R., *Brass 6013*, Feb.–March 1934, alt. 30 m., damp slopes of a savannah ridge, uncommon.

New for New Guinea; previously known from northern and northeastern Australia and New Caledonia northwards and westwards to Ceylon and Japan. Specimens from Ceylon (*S. lateriflora* Boeck.) were referred to *S. zeylanica* Poir. by Thwaites and others, but Poiret's original description refers to a large plant which, from the examination of an excellent piece of the type loaned from herb. Paris, proves to belong to the species previously described by Retz as *Scleria levis* and later described by Nees as *Scleria hebecarpa*. Apparently little attention has been paid to the extensive description in French following the brief Latin diagnosis. The references to *S. zeylanica* in Malaysian and New Caledonian literature really belong to *S. rugosa*. I have seen excellent isotypes of *S. rugosa* and *S. lateriflora*, but the interpretation of *S. pubigera* Makino is based chiefly on specimens so labelled from Taiwan in herb. Melbourne. *Brass 7532 A* was determined by Kükenthal as *Scleria tessellata* Willd. var. *debilis* Benth.; the latter is a common Queensland plant differing from *S. rugosa* in habit and the shape of the nut and disc.

Scleria levis Retz. Obs. **4**: 13. 1786.

Scleria zeylanica Poir. Encycl. Meth. **7**: 3. 1806; **syn. nov.**
Scleria hebecarpa Nees in Wight, Contrib. Bot. Ind. 117. 1834; Valck. Suring. Nova Guin. Bot. **8**: 712. 1912; Palla in Rechinger, Denkschr. Math.-Naturw. Kais. Akad. Wiss. Wien **89**: 500. 1913; Kükenth. Bot. Jahrb. **59**: 58. 1924; Ohwi, Bot. Mag. Tokyo **56**: 212. 1942; **syn. nov.**
Scleria hebecarpa Nees var. *pubescens* (Steud.) C. B. Clarke in Hook f. Fl. Brit. Ind. **6**: 689. 1894; **syn. nov.**

Scleria hebecarpa Nees forma *pilosa* Valck. Suring., Nova Guin. Bot. **8**: 712. 1912; **syn. nov.**
Scleria neesiana Hook. & Arn. Bot. Beechey Voy. 229. 1841; **syn. nov.**
Scleria pubescens Steud. Syn. Cyp. 168. 1855; **syn. nov.**
Scleria japonica Steud. Syn. Cyp. 169. 1855; **syn. nov.**
Scleria vestita Boeck. Linnaea **38**: 482. 1874; **syn. nov.**
Scleria dietrichiae Boeck. Flora **58**: 121. 1875; **syn. nov.**
Scleria wichurai Boeck. Bot. Jahrb. **5**: 510. 1884; **syn. nov.**

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7877*, Sept. 1936, occasional on wet grass plains (clumps 80 cm. high); Lake Daviumbu, Middle Fly R., *Brass 7691*, Sept. 1936, savannahs, common on swamp margins; Gaima, Lower Fly R. (east bank), *Brass 8264*, Nov. 1936, open savannah-forest, plentiful on hard soils; Tarara, Wassi Kussa River, *Brass 8715*, Jan. 1937, common grass associate, savannah-forest ridges; Dagwa, Oriomo R., *Brass 5996*, Feb.–March 1934, alt. 40 m., amongst grasses on a savannah ridge.

This species has not previously been recorded for Papua, though it is widely spread from Queensland and New Caledonia to India and Japan. It is the species commonly known as *Scleria hebecarpa* Nees, but examination of the type of *Scleria levis* Retz. (LD) and of a piece of the type of *Scleria zeylanica* Poir. (P) has shown that these three names are synonymous. For some inexplicable reason, Poiret's name has been almost invariably associated with *S. lateriflora* Boeck. (which is *S. rugosa* R. Br.) in spite of the fact that Poiret's description refers to a much larger and otherwise different plant (see also under *S. rugosa*). The name *Scleria levis* (the epithet of which is often spelled *laevis*) has been commonly applied to specimens of *S. terrestris* (L.) Fassett on which the fruits are somewhat depressed due to imperfect development.

Brass 8264 had been determined as *Scleria hebecarpa* Nees by Kükenthal. *Brass 7691, 8715* represent the more or less hairy form described as *S. hebecarpa* Nees var. *pubescens* (Steud.) C. B. Clarke (and were determined as such by Kükenthal), *S. pubescens* Steud. and *S. vestita* Boeck.

Scleria ciliaris Nees in Wight, Contrib. Bot. Ind. 117. 1834.

Scleria chinensis Kunth, Enum. Pl. **2**: 357. 1837.
Scleria bancana Miq. Fl. Ind. Bat. Suppl. 602. 1860; Valck. Suring. Nova Guin. Bot. **8**: 712. 1912; Kanehira, Jour. Dept. Agr. Kyushu Univ. **4**: 282. 1935; Kükenth. Bot. Jahrb. **69**: 261. 1938; Ohwi, Bot. Mag. Tokyo **56**: 212. 1942; **syn. nov.**
Scleria malaccensis Boeck. Linnaea **38**: 507. 1874; K. Schum. in Warb. Bot. Jahrb. **13**: 266. 1891: **syn. nov.**

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7670*, Sept. 1936, rain-forest, occasional clumps 1.2–1.5 m. high, along margin of lake (det. Uittien as *S. hebecarpa* Nees); Gaima, Lower Fly R. (east bank), *Brass 8252*, Nov. 1936, common grass associate in savannah forests (det. Uittien as *S. hebecarpa* Nees); Wuroi, Oriomo R., *Brass 5808*, Jan.–March 1934, alt. 10 m., amongst tall grass on edge of rain-forest. Gulf Division: Kerema, *Brass 1207*, March 1926, open grassland near coast, in clumps 1 m.

high. Central Division: On range between Sogere and Javararie, *White 317*, July–Aug. 1918; Astrolabe Range, *White 218*, July–August 1918, in grassland; Astrolabe Range, *Armit* (MEL). Eastern Division: Cloudy Mts., *Chalmers* (MEL).

SOLOMON ISLANDS: Mariga Island: N'Gela, *Brass 3486*, Jan. 1933, small sedge on grasslands.

New for Papua and the Solomon Islands; extends from northern Queensland northwards and westwards to Ceylon, India and China.

One state of this species has been generally called *Scleria chinensis* since the time of Kunth. Kunth proposed this name to replace *Scleria ciliaris* Nees "because of the earlier name of Michaux." But the name for the American species proposed by Michaux is *Scleria ciliata*. The suffixes *-tus* (*-ta*, *-tum* = provided with) and *-ris* (*-re* = of or belonging to) have quite distinct meanings, so that the two epithets *ciliata* and *ciliaris* (and consequently the names of which they form part) must be treated as distinct (International Code of Botanical Nomenclature, Art. 82, and Rec. 821); they are not orthographic variants. Kunth's action was therefore unjustified and merely created a superfluous name. The name proposed by Nees is the correct one.

Scleria malaccensis is the same form as *S. bancana* and has usually been distinguished on the grounds that the leaves of *S. ciliaris* (*S. chinensis*) are scattered and have more or less distinctly winged sheaths while *S. bancana* has the middle leaves approximated in pairs with usually unwinged sheaths, even though *S. bancana* was originally described as having winged sheaths. The specimens cited above show a continuous series between the two extremes.

I have not been able to identify *Scleria chinensis* Kunth var. *biauriculata* C. B. Clarke in Hook. f. Fl. Brit. Ind. **6**: 690. 1894. The description could refer to members of the series just mentioned; the synonym cited, *S. exaltata* Boeck., belongs to *S. terrestris*; one of the two collections cited is also cited as belonging to the typical form of *S. chinensis* and the other may or may not be Boeckeler's type.

Scleria macrophylla Presl has been referred to *S. chinensis* by some authors, but this name refers to an American species (Core, Brittonia **2**: 37–8. 1936).

Scleria terrestris (L). Fassett, Rhodora **26**: 159. 1924.

Zizania terrestris L. Sp. Pl. ed. 1: 991. 1753.
Diaphora cochinchinensis Lour. Fl. Cochinch. 578. 1790.
Olyra orientalis Lour. Fl. Cochinch. 552. 1790.
Scleria elata Thw. Enum. Pl. Zeyl. 353. 1864; K. Schum. Notizbl. Bot. Gart. Mus. Berlin **2**: 98. 1898; Lam, Nat. Tijds. Nederl. **88**: 194, 203, 207. 1928.
Scleria melanostoma Nees ex Boeck. Linnaea **38**: 514. 1874.
Scleria exaltata Boeck. Bot. Jahrb. **5**: 511. 1884; **syn. nov.**
Scleria hasskarliana Boeck. Bot. Jahrb. **5**: 511. 1884; **syn. nov.**
Scleria haematostachys Boeck. Bot. Jahrb. **5**: 512. 1884; **syn. nov.**
Scleria doederleiniana Boeck. Bot. Jahrb. **5**: 512. 1884; **syn. nov.**

Scleria ploemii Boeck. Bot. Jahrb. **5**: 513. 1884; **syn. nov.**
Scleria luzonensis Palla, Allg. Bot. Zeitschr. **13**: 49. 1907; **syn. nov.**
Scleria cochinchinensis (Lour.) Druce, Rept. Bot. Exch. Club Brit. Isles **4**: 646. 1917.
Scleria chinensis Kunth var. *luzonensis* (Palla) Uitt. Rec. Trav. Bot. Néerland. **32**: 201. 1935 et Meded. Bot. Mus. Herb. Rijksuniv. Utrecht **17**: 201. 1935; **syn. nov.**
Scleria chinensis Kunth var. *luzonensis* (Palla) Uitt. forma *pilosa* Uitt. ll.cc.; **syn. nov.**

NETHERLANDS NEW GUINEA: 4 km. SW. of Bernhard Camp, Idenburgh R., *Brass 13480*, March 1939, alt. 850 m., one clump on an open landslip.

NORTH-EAST NEW GUINEA: Morobe District: Belung R. to Sarawaket, *J. & M. S. Clemens 4875*, Jan. 1937.

PAPUA: Central Division: Port Moresby, *Lawes* in 1884 (MEL); Sogere, *White 308*, July–Aug. 1918; Urunu, Vanapa Valley, *Brass 4779*, July–Aug. 1933, alt. 1900 m., in clumps amongst tall weed grass on old garden land, common.

New for Papua; extends from Queensland to India and southern China.

This is the species commonly known as *Scleria elata* Thw. The name *Scleria terrestris* is based on *Zizania terrestris* L., which is based on *Katu-Tsjolam* Rheede, Hort. Mal. 12: 113, *t. 60*. 1703, and this evidently refers to a *Scleria*; C. B. Clarke in Hook. f. Fl. Brit. Ind. **6**: 685–694. 1894 recorded only *S. elata* Thw. and *S. hebecarpa* Nees from the region covered by Rheede, and Rheede's figure could only refer to *S. elata*. *Scleria cochinchinensis* is based on *Diaphora cochinchinensis* Lour., the type of which was seen by Merrill (see Trans. Am. Phil. Soc. n.s. **24**: 89. 1935). *Olyra orientalis* Lour. is referred here on Merrill's suggestion, l.c., 90. I have seen syntypes of *Scleria elata* (MEL), *S. hasskarliana* (MEL), *S. luzonensis* (BRI, NSW, L) and possibly of *S. ploemii* (L). *Thwaites 3031*, cited by Boeckeler as the type of *S. exaltata*, is represented at Melbourne, but the specimen differs considerably from Boeckler's description in being much smaller and having differently shaped disc-lobes; it belongs to *S. levis* Retz. (*S. hebecarpa* Nees).

Scleria scrobiculata Nees & Meyen in Wight, Contrib. Bot. Ind. 117. 1834; K. Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee 198. 1901 (at most only partly); Valck. Suring. Nova Guin. Bot. **8**: 712. 1912 (at most only partly); Kükenth. Bot. Jahrb. **59**: 58. 1924, partly; ? Kanehira, Jour. Dept. Agr. Kyushu Univ. **4**: 282. 1935; (?) Ohwi, Bot. Mag. Tokyo **56**: 212. 1942.

Scleria timorensis Nees, Linnaea **9**: 303. 1834.
Scleria purpureovaginata Boeck. Bot. Jahrb. **5**: 513. 1884; K. Schum. in Warb. Bot. Jahrb. **13**: 266. 1891; Valck. Suring. Nova Guin. Bot. **8**: 713. 1912; **syn. nov.**
Scleria keyensis K. Schum. in Warb. Bot. Jahrb. **13**: 267. 1891; Valck. Suring. Nova Guin. Bot. **8**: 713. 1912.
Scleria suffulta C. B. Clarke, Kew Bull. Add. Ser. **8**: 58. 1908; **syn. nov.**

PAPUA: Western Division: New Guinea, near Dutch boundary, *MacGregor* in 1890 (MEL); Fly R., *D'Albertis* (MEL); Lake Daviumbu, Middle Fly R., *Brass 7715*, Sept. 1936, mixed with grass fringing shore of savannahs, clumps 2–2.5 m. high (det. Kükenthal); Daru Island, *Brass 6244*, March 1936, common with grasses on damp soil of savannah forests (det. Kükenthal as *Scleria chinensis* Kunth). Central Division: Port Moresby, *Goldie* (MEL); towards Owen Stanley Range, *Goldie* in 1878 (MEL); Astrolabe Range, *Armit* in 1883, scrubs (MEL).

New for Papua, and perhaps for New Guinea. The species is widely spread in Malaysia, extending into Queensland and apparently to China. At least some of the records of this species for New Guinea belong properly to *Scleria polycarpa* (see under this species), but I have not seen many of the specimens on which the records are based.

Scleria polycarpa Boeck. Linnaea **38**: 508. 1874.

Scleria margaritifera Willd. Sp. Pl. **4**: 312. 1805; Rendle in Gibbs, Phyt. Fl. Arfak Mts. 200. 1917; non Gaertn. 1788; **syn. nov.**

Scleria graeffeana Boeck. Flora **58**: 121. 1875; K. Schum. in Warb. Bot. Jahrb. **13**: 266. 1891; Valck. Suring. Nova Guin. Bot. **8**: 712. 1912; Palla in Rechinger, Denkschr. Math.-Naturw. Kais. Akad. Wien **89**: 500. 1913; **syn. nov.**

Scleria ternifolia Domin, Biblioth. Bot. **85**: 490. 1915; **syn. nov.**

NETHERLANDS NEW GUINEA: Bernhard Camp, Idenburg R., *Brass 13937*, April 1939, alt. 50 m., abundant in sago and other permanently swampy forest of river plain, 2–3 m. high.

NORTH-EAST NEW GUINEA: New Ireland: W. coast, *Bradtke 125*, May 1917, 0 m. (NSW). Duke of York Island, *Bradtke 185*, May 1917, secondary bush, grassfields (NSW). Morobe District: Augustusfluss (= Sepik R.) *Hollrung 815* (MEL, L); Huon Gulf, *Lauterbach 1185* (MEL).

PAPUA: Western Division: New Guinea, near Dutch boundary, *MacGregor* in 1890 (MEL); Fly R., *Bäuerlen 514*, Nov. 1885, on red clay banks; Lake Daviumbu, Middle Fly R., *Brass 7590*, Aug. 1938, forming dense thickets 2.5–3 m. high, in edge of forest along lake shores (det. Kükenthal as *S. scrobiculata* Nees); Lake Daviumbu, Middle Fly R., *Brass 7663*, Sept. 1936, savannahs, scattered clumps 1.5 m. high on swamp margins (det. Kükenthal as *Scleria chinensis* Kunth); Lower Fly R., east bank opposite Sturt Island, *Brass 8115*, Oct. 1936, tufted in semi-shade on edge of sago swamps (det. Kükenthal as *S. scrobiculata* Nees). Gulf Division: Ghu, Vaitata R., *Brass 938*, Feb. 1926, rain-forest borders, small clumps 2–3 ft. high. Central Division: Boku, *Schlenker 9*, July 1909; Deva Deva, *White 588*, alt. about 1200 m., July–August 1918 (large sedge about 6 ft. high); Kubuna, *Brass 5563*, Nov. 1933, alt. 100 m., common amongst ferny ground cover in rain-forest; Astrolabe Range, *White 359*; Sogere, *White 370*, July–August 1918; Bisiatabu, *Brass 584*, Nov. 1925, alt. 1500 ft., banks of streams; Owen Stanley Range, between Mts. Brown and Clarence, *Brass 1479*, May 1926, alt. 4000 ft. Eastern Division: Fife Bay, *Turner 95*, Sept. 1930 (plant about 4 ft. high); South Cape, *Chalmers* (MEL); "south-east New Guinea," *Chalmers* in 1878; Samarai, *Fitzgerald 7*, common (more or less caespitose, 1–3 ft. high); Dixon's Bay, Rossel Island, *Chalmers & Bridge*, Jan. 1885; islands near the south-east coast, *Armit* in 1884.

SOLOMON ISLANDS: Without definite locality, *Wernhem*, Jan. 1911 (NSW).

NEW HEBRIDES: Without definite locality, *Haer 65* in 1902 (NSW).

Widely spread from New Guinea and Queensland through Melanesia to eastern Polynesia. Not previously recorded from the Solomon Islands.

This species has usually been called *Scleria margaritifera* Willd., which is a later homonym of *Scleria margaritifera* Gaertn., a name that has been overlooked by most botanists and by the compilers of Index Kewensis. Gaertner gave a good account and figure of a portion of the inflorescence, spikelets and fruit. He cited several synonyms, including *Carex lithosperma* L. and *Scleria flagellum-nigrorum* Berg. Core, Brittonia **2**: 87. 1936, referred Gaertner's name, figure and description to *S. flagellum-nigrorum* Berg., which would seem to be its correct disposition; it is accordingly a superfluous name for this species. Willdenow, Sp. Pl. **4**: 312. 1805, cited *S. margaritifera* Gaertn. as one of the synonyms of "*Scleria flagellum* Sw.," but on the next page deliberately used the same name for a species which he described as new from a specimen collected by Forster on the island of Tanna. Hence *Scleria margaritifera* Gaertn. and *Scleria margaritifera* Willd. are quite distinct names, and both of them are illegitimate under any circumstance.

I have not seen the types of *S. polycarpa, S. graeffeana* or *S. ternifolia*, but I have seen specimens from the type-localities of each that agree with the original descriptions. The species is closely allied to *S. scrobiculata* Nees, differing from it chiefly in the narrower partial panicles with fewer and less spreading branches, the inconspicuous bracteoles shorter than the spikelets, the relatively inconspicuous male spikelets, the more evenly distributed fertile spikelets, the nut more gradually narrowed to the tip and nearly smooth to slightly rugulose at maturity, and the less deeply divided disc with more prominently denticulate margins; the nuts are frequently bright blue with red discs. The leaf-sheaths in both species may be broadly or narrowly winged or quite wingless on different individuals. Both species are robust plants with the middle leaves in false-whorls of three, relatively numerous partial panicles, medium-sized nuts which are also more or less hirtellous, and rather short discs.

The following references to *Scleria scrobiculata* belong wholly or in part to *S. polycarpa*: K. Schum. & Hollr. Fl. Kaiser Wilhelmsl. 25. 1889; K. Schum. & Lauterb. Fl. Deutsch. Schutzgeb. Südsee 198. 1901; F. M. Bail. Queensl. Agr. Jour. **23**: 220. 1909; Valck. Suring. Nova Guin. Bot. **8**: 712. 1912; Kükenth. Bot. Jahrb. **59**: 58. 1924.

Scleria poaeformis Retz. Obs. **4**: 13. 1786.

Scleria oryzoides Presl, Rel. Haenk. **1**: 201. 1830; F. Muell. Pap. Pl. **2**: 51. 1886.

PAPUA: Western Division: Fly R., *Bäuerlen 562*, Nov. 1885 (MEL); Lake Daviumbu, Middle Fly R., *Brass 7855*, Sept. 1936, in dense pure stands dominating many large swamps on savannahs; Gaima, Lower Fly R. (east bank),

Brass 8261, Nov. 1936, swamps in savannah forest area; Wuroi, Oriomo R., *Brass 5748*, Jan.–March 1934, alt. 10–30 m., in dense formation in a small swamp; Daru Island, *Brass 6338*, March 1936, forming pure stands, 1.5 m. tall, in shallow open swamp in savannah forest.

Bäuerlen's specimens were cited by F. Mueller, l.c.; Brass's specimens were received determined by Kükenthal as *S. oryzoides* Presl. My recent examination of the type of *S. poaeformis* (LD) confirmed the opinion expressed by C. E. C. Fischer in Kew Bull. **1931**: 265. 1931 that this name and *S. oryzoides* are synonymous. The species extends from northern Queensland northward and westward to India.

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Besides the species mentioned in the foregoing pages, the following have been recorded for New Guinea, based on specimens that I have not seen:

Scleria hookeriana Boeck.; Kükenth. in Eng. Bot. Jahrb. **59**: 59. 1924.

Scleria levis Retz. forma *villosa* Valck. Suring. Nova Guin. Bot. **8**: 712. 1912; Kükenth. Bot. Jahrb. **59**: 58. 1924; Ohwi, Bot. Mag. Tokyo **56**: 212–3. 1942.

Scleria brownii Kunth: Kükenth. Bot. Jahrb. **70**: 464. 1940.

The record of *S. brownii* is very likely based on specimens of *S. novae-hollandiae* (see under this species); the other records may also be based on specimens of species discussed elsewhere in this paper.

The following key will serve to distinguish the species seen from New Guinea:

Spikelets — at least the fertile ones — androgynous; disc reduced to an indistinct basal rim or (in *S. motleyi*) more or less cupshaped and thin; nut trigonous.
  Annual, lemon-scented; spikelets in small distant clusters along a simple common axis without prominent bracts . . . *S. pergracilis.*
  Perennial; inflorescence of terminal and axillary partial panicles with prominent bracts, the partial panicles sometimes spike-like.
    Disc rudimentary; nut glabrous.
      Nut quite smooth, even when young . . . . . *S. lithosperma.*
      Nut rugose, even at extreme maturity . . . . . *S. roxburghii.*
    Disc cup-shaped; nut hirtellous with ferruginous hairs . . . . . *S. motleyi.*
Spikelets unisexual, the females commonly with one or more empty glumes above the flowers; disc always present, shallowly to deeply 3-lobed; nut not distinctly angular.
  Annual plants rarely up to 50 cm. high; culms about 1 mm. wide or less; leaves 1–3 mm. wide.
    Nut ellipsoid or cylindroid, not prominently apiculate; terminal partial panicle longer than the others.
      Disc deeply divided with nearly separate ovate to oblong, more or less acute lobes; nut deeply tessellate, more or less shining . . *S. tessellata.*
      Disc small and thin, shallowly lobed with broadly rounded lobes; nut dull, smooth or somewhat verrucose or somewhat reticulate . . . . . *S. novae-hollandiae.*

Nut globular, prominently apiculate, at first reticulate, finally often smooth except for a few tubercles on the upper part; disc thick, shallowly lobed; partial panicles all small ..... *S. rugosa.*

Perennials up to 3 m. high or more with prominent rhizomes; culms at least 1.5 mm. wide and usually wider; leaves 4–20 mm. wide.

Spikelets mostly in pairs, the lower one of most pairs fertile; inflorescence of 3–8 partial panicles, the lower ones from long, leaf-like bracts; leaves long-tapering to a narrowly obtuse or filiform tip; rhizome more or less knotty with approximated culms.

Ligule longer than (usually 2–3 times as long as) wide; bracteoles unusually prominent and long exserted from the dense partial panicles ..... *S. ciliaris.*

Ligule shorter (usually much shorter) than wide; bracteoles usually less prominent, or setaceous; partial panicles looser-flowered or subspiciform.

Leaves all about equally distributed along the culm; bracteoles prominent.

Disc-lobes lanceolate, more or less acute, more or less toothed ..... *S. levis.*

Disc-lobes broadly rounded, entire ..... *S. terrestris.*

Leaves clustered in groups of 3 (rarely 2) at the base of and below the inflorescence.

Bracteoles nearly as long or as long as the more or less spreading branches of the partial panicles; nuts borne chiefly towards the base of the branches, abruptly rounded below the mucronate tip, commonly deeply scrobiculate and white .. *S. scrobiculata.*

Bracteoles inconspicuous, much shorter than the more or less erect branches of the more or less spiciform partial panicles; nuts evenly distributed throughout the partial panicles, rather gradually narrowed to the mucronate tip, rugulose to smooth at maturity, often tinged blue; disc often red ..... *S. polycarpa.*

Spikelets not paired, evenly distributed along the branchlets, the fertile ones restricted to the lower part of the lower branches; inflorescence of a single pedunculate compound compact terminal panicle; leaves broad, scarcely tapering to the obtusely rounded tips; rhizome elongated with rather distant culms ..... *S. poaeformis.*

Diplacrum R. Brown

Diplacrum caricinum R. Br. Prodr. 241. 1810.

Scleria caricina (R. Br.) Benth. Fl. Austral. **7:** 426. 1878; Kükenth. Bot. Jahrb. **69:** 261. 1938.
Scleria axillaris Moon, Catal. Pl. Ceylon 62. 1824, *nomen nudum.*
Diplacrum tridentatum Brogn. Duperr. Voy. Bot. *t. 26.* 1826.
Diplacrum zeylanicum Nees in Wight, Contrib. Bot. Ind. 119. 1834.
Olyra malaccensis Wall. ex Kunth, Enum. Pl. **2:** 360. 1837, pro syn.

PAPUA: Western Division: Lake Daviumbu, Middle Fly R., *Brass 7842*, Sept. 1936, common on wet plains, also in edge of *Tristania* forests.

New for Papua; widely distributed in Malaysia, extending into Ceylon, India, South China and Queensland.

The limits of *Diplacrum* and *Scleria* have been variously circumscribed and the two groups have often been treated as congeneric. A few American species have sometimes been referred to *Diplacrum*, but they are best treated as a separate genus, *Peteroscleria* Nees. The more important characters differentiating the three genera are as follow:

Scleria: Male spikelets (or male portion of androgynous spikelets) borne above the female; stamens commonly 3. Female spikelet: glumes 3–6 below the flower and usually one or more reduced ones above, 1-nerved, the keel not winged, entire at the tip, permanently membranous, persistent after the fall of the ripe nut. Nut smooth or variously reticulate or tuberculate or transversely rugose, the transverse ribbing at least as prominent (usually more prominent) than the vertical. Outer disc usually present. Leaves in the middle of the stem much the longest, the uppermost (bracts of partial panicles) gradually much shorter and narrower, the lower ones gradually reduced to bladeless sheaths. Partial inflorescences in the upper part of the stem, or inflorescence entirely terminal.

Diplacrum: Male spikelets borne below the female; stamen commonly one. Female spikelet: glumes 2, 3–7-nerved, keeled but the keel not winged, more or less 3-lobed or 3-toothed, hardened at maturity and commonly falling with the ripe nut which they enclose; no glumes above the flower. Nut tending to be heavily ribbed vertically, transverse ribs less pronounced or irregular or absent. Outer disc absent. Leaves or bracts all very similar, all or nearly all with axillary heads of spikelets, 1 or 2 basal ones sometimes reduced to sheaths.

Pteroscleria: Male spikelets below the female; stamens commonly 3 in the lower flowers. Female spikelet: glumes 2, the keel prominently winged, otherwise nearly nerveless, entire at the tip, not hardened at maturity (?), persistent (?); no glumes above the flower. Nut tending to be ribbed vertically, but the ribbing faint or obscure. Outer disc absent. Leaves dissimilar, only the upper ones with axillary heads of spikelets.

As thus delimited, *Diplacrum* comprises a group of about five small slender annual species of the Old World Tropics. *Diplacrum caricinum* is the type-species and is the most widely spread. Endemic species occur in Malaya (*D. reticulatum* Holttum), Africa (*D. africanum* C. B. Clarke) and Australia (*D. pygmaeum* [R. Br.] Nees ex Boeck. and another).

Uncinia Persoon

Uncinia riparia R. Br. Prodr. 241. 1810.

NETHERLANDS NEW GUINEA: Mt. Wilhelmina, 7 km. NE. of Wilhelmina-top, *Brass & Meyer-Drees 9847*, Sept. 1938, alt. 3560 m., common in weak clumps on mossy floor of subalpine forest.

PAPUA: Central Division: Mt. Albert Edward, *Brass 4415*, May–July 1933, alt. 3680 m., sporadic on floor of forest.

New for New Guinea; previously known from New Zealand, Tasmania and the mountains of the extreme SE. Australian mainland.

The previous records of *Uncinia riparia* from New Guinea refer to other species. That of F. Mueller, Trans. Roy. Soc. Vict. 1 (2): 36. 1889 and of Kükenthal, Pflanzenr. 4 (20), 38: 63. 1909 and Bot. Jahrb. 59: 59. 1924 refer to specimens of *U. sclerophylla* Nelmes, Kew Bull. 1949: 143. 1949. According to Nelmes, l.c., pp. 142–5, Kükenthal's reference in Bot. Jahrb. 69: 261. 1938 was based on collections in which *U. sclerophylla* Nelmes, *U. subtrigona* Nelmes and perhaps another species are represented. The Clemens collections are so badly mixed and sometimes so poor that it is very risky to interpret references by the examination of alleged duplicates.

ADDENDA

In a parcel of old specimens from New Guinea received for determination from the Melbourne Herbarium there were found a specimen of an undescribed species of *Hypolytrum* and a specimen of a species of *Cyperus* previously unrecorded from New Guinea. They are discussed here, together with other corrections and additions to the previous contributions.

Hypolytrum L. C. Richard

Hypolytrum microcarpum sp. nov. PLATE I.

Culmi e rhizomate brevi caespitosi, circa 50 cm. alti, 2 mm. crassi, triquetri, lateribus concavis striati, angulis anguste obtusis prope apicem scaberuli, ceterum laeves. Folia basalia linearia, chartacea, 6–9 mm. lata, usque 37 cm. longa, basim versus complicata haud vel vix angustata, apice acutata, prope apicem marginibus nervoque mediano scabra, ceterum laevia; folia caulina 2, conspicue vaginantia, summum inflorescentiam superans, basalibus simillima nisi basim versus angustata. Bracteae inferiores foliiformes, inflorescentiam superantes. Inflorescentia suboblonga, subcorymbosa, circa 5 cm. longa lataque, multiflora; axis communis angulosa scabra; rami divaricati, usque ad 22 mm. longi, compressi, scabri, prope apicem corymboso-ramosi ramulis nonnullis eodem modo divisis; ramuli ultimi (pedicelli) usque ad 5 mm. longi, filiformes. Spiculae fusco-brunneae obovoideae vel oblongae, 3.5–4 mm. longae, sub flore circa 2 mm. sub fructu circa 3 mm. latae, pauciflorae. Glumae (explanatae) orbiculari-obovatae, muticae, brunneae, marginibus (apice ipso excepto) subscariosae, 1.3–1.5 mm. longae. Flores 1.3 mm. longi; squamellae more generis 2, liberae, carina parce ciliatae, explanatae lanceolatae obtusae, circa 1.3 mm. longae. Nux subglobosa, leviter compressa, circa 1.4–1.5 mm. longa, 1.3–1.4 mm. lata, brevissime umbonato-rostrata, bicostulata, irregulariter laxeque ruguloso-reticulata, dilute flavo-brunnea sed creberrime rubro-punctata.

HYPOLYTRUM MICROCARPUM S. T. BLAKE

PAPUA: Eastern Division: Cloudy Mountains near South Cape, *Chalmers & Bridge* in 1884 (TYPE in MEL).

The description is based on a single specimen consisting of a fruiting culm and two innovation-shoots all attached to the rhizome. It has the habit and general appearance of *H. latifolium* L. C. Rich., *H. scirpoides* (Presl) Merr. (*H. philippense* C. B. Clarke), *H. scabrum* Uitt. and *H. vitiense* C. B. Clarke, but it differs from all of these in the much smaller spikelets, glumes, flowers and nuts and the nearly globular nut with its beak reduced to a very small umbo. The nearly smooth leaves and stem further distinguish it from *H. scirpoideum* and *H. scabridum* and the wrinkling on the nut from *H. vitiense*. It must also be closely allied to *H. minus* Ridl.; I have seen no specimen of this species, and although Ridley's description leaves much to the imagination, the stress placed on the scabrous margins of the much broader leaves suggests that it is closer to *H. scirpoideum* or identical with this, as suggested by Kükenthal, Bot. Jahrb. **59**: 53. 1924.

Cyperus Linnaeus

Cyperus cinereobrunneus Kükenth. Mitteil. Thüring. Bot. Ver. N. F. **50**: 3. 1943; Kükenth. ex S. T. Blake, Jour. Arnold Arb. **28**: 216. 1947.

I had not seen Kükenthal's paper when I published his name in 1947.

Cyperus globosus All.; S. T. Blake, Jour. Arnold Arb. **28**: 220. 1947.

Cyperus globosus All. var. *oblonginux* Kükenth. Mitteil. Thüring. Bot. Ver. N. F. **50**: 7. 1943.

I had mentioned (l.c.) that, in the determination on the label, Kükenthal had distinguished *Brass 8309* as a variety; I had not then seen the description. These plants seem to be no more than an individual variation.

Cyperus fulvus R. Br. var. **confusus** (C. B. Clarke) Kükenth. Pflanzenr. **4 (20), 101**: 456. 1936.

Mariscus fulvus (R. Br.) C. B. Clarke var. *confusus* C. B. Clarke ex Domin, Biblioth. Bot. **85**: 444. 1915.

PAPUA: Central Division: Quaipo, *MacGregor* in 1889 (MEL).

The species is new for New Guinea, but is common and widely spread

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PLATE I

Hypolytrum microcarpum S. T. Blake. Type specimen × about ½ with analytical drawings. Fig. 1. Glume. Fig. 2. Nut. Fig. 3. Transverse section of nut. All figures × about 10. Analytical drawings by S. T. Blake, photography by G. Cripps, Photographic Section, Department of Agriculture and Stock, Brisbane.

in NE. Australia. Although quite variable, it is doubtful how much importance can be assigned to the varieties that have been described.

Schoenus Linnaeus

Schoenus maschalinus R. & S. Syst. Veg. 2: 77. 1817; S. T. Blake, Proc. Roy. Soc. Queensl. 60: 47. 1950.

Schoenus foliatus (Hook. f.) S. T. Blake; S. T. Blake, Jour. Arnold Arb. 29: 93. 1948.

Later botanists have overlooked the fact that Roemer and Schultes correctly gave a new name to *Chaetospora axillaris* R. Br. when this was transferred to *Schoenus*. An extensive and complicated synonymy has become associated with the species, which has been discussed in my papers cited above.

Rhynchospora Vahl

Rhynchospora triflora Vahl; S. T. Blake, Jour. Arnold Arb. 29: 101. 1948.

Rhynchospora triflora Vahl var. *papuana* Kükenth. Bot. Jahrb. 74: 427. 1949.

Rhynchospora triflora var. *papuana* was founded entirely upon *Brass 8356*; I cannot distinguish our specimen of this from our specimen of *Henderson in Singapore Field no. 24101* which Kükenthal cited under *R. triflora*.

Carex Linnaeus

Several emendations to my determinations in Jour. Arnold Arb. 28: 99–116. 1947 appeared in a paper by E. Nelmes in Kew Bull. 1949: 378–386. 1949. This was followed by a revision of the Malaysian species in Reinwardtia 1: 221–450. 1951. As pointed out in the introduction to my paper, I had to place considerable reliance on descriptions only; Mr. Nelmes has had a much wider experience in this genus, and his opinions should have preference.

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PREVERNAL LEAFING OF ASPEN IN UTAH MOUNTAINS

WALTER P. COTTAM

With two plates

THE ROCKY MOUNTAIN ASPEN (*Populus tremuloides Michx., var. aurea* Tidestrom) dominates more mountainous terrain in Utah at elevations between 7,000 and 10,000 feet than any other forest species. Several features of its growth-form, together with its peculiar autecology and synecology, make this species a very conspicuous forest type. Unlike all other prominent forest species with which it may be associated, such as Douglas fir, white fir, alpine fir, blue spruce, Engelmann spruce, ponderosa pine and lodgepole pine, the aspen is deciduous in habit.

Often the aspen occurs in almost pure stands, which may vary in size from a few square rods to several square miles of solid forest. But whether small or large, the aspen stands are sharply discontinuous, single aged and usually dense. The shiny green leaves of summer, the multi-colored shades of yellow in autumn, and the slender, straight, white boles at all seasons of the year are features of the aspen that set it apart in contrast to all contiguous association types, whether mountain conifers or browse.

But the contrast that exists between the aspen stands and other mountain vegetation types is often exceeded, in early spring at least, by striking differences in the time of leafing within the aspen groves themselves. This phenomenon is widespread throughout the mountains of Utah and neighboring states. In early spring almost any aspen forest shows sharply discontinuous colonies of trees that attain full leaf two or three weeks earlier than the major surrounding stand in which at any other time they are likely to remain unnoticed except by the critical observer.

At mid-elevations these colonies of prevernal aspen are usually small in comparison with the forest as a whole, and their outline is variable. Frequently they assume a circular shape, but they may be seen as a narrow, serpentine band bisecting large groves. In general, the position of these prevernal colonies seems to have no correlation with slope, exposure, soil, altitude, or sex of trees, but wherever they occur or whatever shape they may assume, the line that separates them from the retarded major population of trees is sharp, and rarely do the two forms intermingle as individuals.

CONTROLS OF PREVERNAL LEAFING

For years the author has been intrigued with the causes underlying the prevernal leafing of aspen colonies and surprised at the lack of textbook reference to this phenomenon. But few facts of aspen ecology

escaped the critical eye and pen of F. S. Baker, who in 1921 wrote an excellent description of the prevernal leafing of aspen colonies with special reference to the Wasatch Plateau of central Utah. His paper (4), entitled "Two Races of Aspen," points out certain taxonomic differences between early- and late-leafing stands and concludes: "The writer confesses an entire inability to explain the causes of these two widely distributed and closely intermingled races of aspen." Yet throughout the article Baker implies that the causes, whatever they may be, are genetic and never environmental.

There can be little doubt that at least two and probably several races of aspen exist that show striking differences in time of leafing. Evidence of these strains is seen in the variable combinations of certain morphological characters often associated with the physiological functions that regulate leafing response. These morphological characters are sufficiently distinct and constant as to enable one to distinguish the races at the seasons of the year when leaf color and size no longer offer safe clues to their identity. For example, Baker pointed out that in the Wasatch Plateau area boles of the early variety are yellow-green in color in contrast to the powdery-white appearance of the late-leafing variety. The writer has found no exception to this phenomenon throughout the northern half of Utah. This bole color difference is due to the failure of the early-leafing form to produce the usual copious bloom on the bark exterior characteristic of the late-leafing variety.

Another character generally useful in distinguishing the leafing strains of aspen is the pruning habit of the trees. In central and northern Utah, early-leafing aspens in general fail to prune themselves of the lower, small, dead branches on the trunk, thereby presenting an appearance of low vigor and untidiness entirely foreign to the late-leafing strain. (Careful observation, however, discloses that this lack of vigor is more apparent than real.)

Thus, in central and northern Utah, prevernal leafing of aspen is associated with the apparently genetic characters of yellow boles and poor pruning. However, on the Aquarius Plateau of south central Utah, the early-leafing character is associated with white boles and clean pruning, while the late-leafing trees are yellow-boled, non-pruning, a complete reversal of genetic alignment of the northern form.

In distribution within the aspen belt, early-leafing varieties dominate the higher elevations only. At the upper limits of the belt, aspens exist mainly as dwarfed thickets, which are always of the early-leafing forms as distinguished, of course, by the bole color and pruning habit. Conversely, the lower limits of the aspen belt are dominated by late-leafing varieties. Thus the contrast between early- and late-leafing aspens is most pronounced in the spring at mid-elevations, where the two forms are often intermingled as colonies. Here also is found the greatest contrast in autumn, for the early-leafing forms, as a rule, maintain their green color several days longer in the fall than do the late-leafing varieties.

For several years the writer has observed a few areas where contiguous colonies of early- and late-leafing aspen fail to present the morphological

differences mentioned above. In all of these exceptions the boles of both aspen groups are white and well pruned, yet the length of the leafing time differences is the usual two to three weeks. One such area is located at the head of South Willow Creek Canyon in the Stansbury Mountains, approximately fifty miles west of Salt Lake City. Another is found in the Abajo Mountains west of Monticello in southeastern Utah. Both areas occur at an elevation of about 7,500 feet.

TEMPERATURE CONTROLS OF PREVERNAL LEAFING

The Stansbury group appears at the bottom of an east-west canyon at a point where the generally straight canyon forks abruptly. The major fork heads south and in a circuitous manner drains the summit of the 10,000 foot range. The minor fork proceeds west for approximately one mile where it ends more or less abruptly, forming a sort of "boxed" segment rather well protected from air drainage from the summit above. Each spring in late May, aspens in this box canyon may be seen in almost full leaf with a sharp line scarcely more than a rod wide bisecting the grove and separating those in leaf from a half mile area of leafless aspens lying at and below the confluence of the major south fork.

Here there is an anomalous condition in which a grove of aspens leaf out considerably before their neighbors two to three hundred feet below them in elevation. In order to ascertain whether temperature might be a controlling factor in this phenomenon, a transect of four stations (two above and two below the leafing line) was established. Recording thermographs, fastened to the aspen branches ten feet above the ground and protected by white canvas tents, were used in this preliminary experiment, as well as in others to be reported below. Readings were begun May 7 and terminated May 19, 1951. During this period neither group of aspen had progressed beyond the swollen bud stage. Figure I shows the daily minimum, maximum and mean temperatures in both aspen groups over this period of 13 days.

The comparative summaries given in Figure I leave little doubt that these two major stands of aspen, showing marked differences in the time of leafing, exist under strict temperature controls and are not separate races. Considering the fact that the early-leafing aspen while occupying the higher elevations show a daily mean temperature two to three degrees greater than the late-leafing stands, these temperature differences seem highly significant. Translated into altitudinal effects, the temperature difference between these two aspen groups is equivalent to approximately 1000 feet in elevation. Furthermore, observations in this area in early June, 1951, disclosed several typical prevernal colonies of genetically controlled aspen within the major retarded zone of lower temperature. These small isolated colonies of yellow-boled aspen came into leaf at approximately the same time as the large stand of white-boled aspen of the higher temperature area.

GENETIC CONTROLS OF PREVERNAL LEAFING

Circumstances prevented the writer from visiting the prevernal leafing aspen colonies of the Abajo Mountains of southeastern Utah until August, 1951. With the aid of kodachrome pictures taken in May, 1950, the exact position of these colonies was ascertained. Comparative temperature records were taken for a period of four days. No significant temperature differences between the early-leafing and late-leafing stands were found. The uniformity of the topographical features suggests, moreover, that there should be none. While considerably more temperature data are needed for this area, the evidence points to the probability that early-leafing and late-leafing colonies of aspen here represent different genetic strains unassociated with observable bole and pruning characters.

Continuous temperature data from June 1 to September 30, 1951, except for two interruptions of four days each, were secured from contiguous colonies of prevernal and late-leafing aspen at Mt. Timpanogos located in the Wasatch Range 30 miles southeast of Salt Lake City. These colonies, occupying mid-altitudinal positions of about 8,000 feet, all showed the morphological differences described earlier, as well as the

FIGURE I

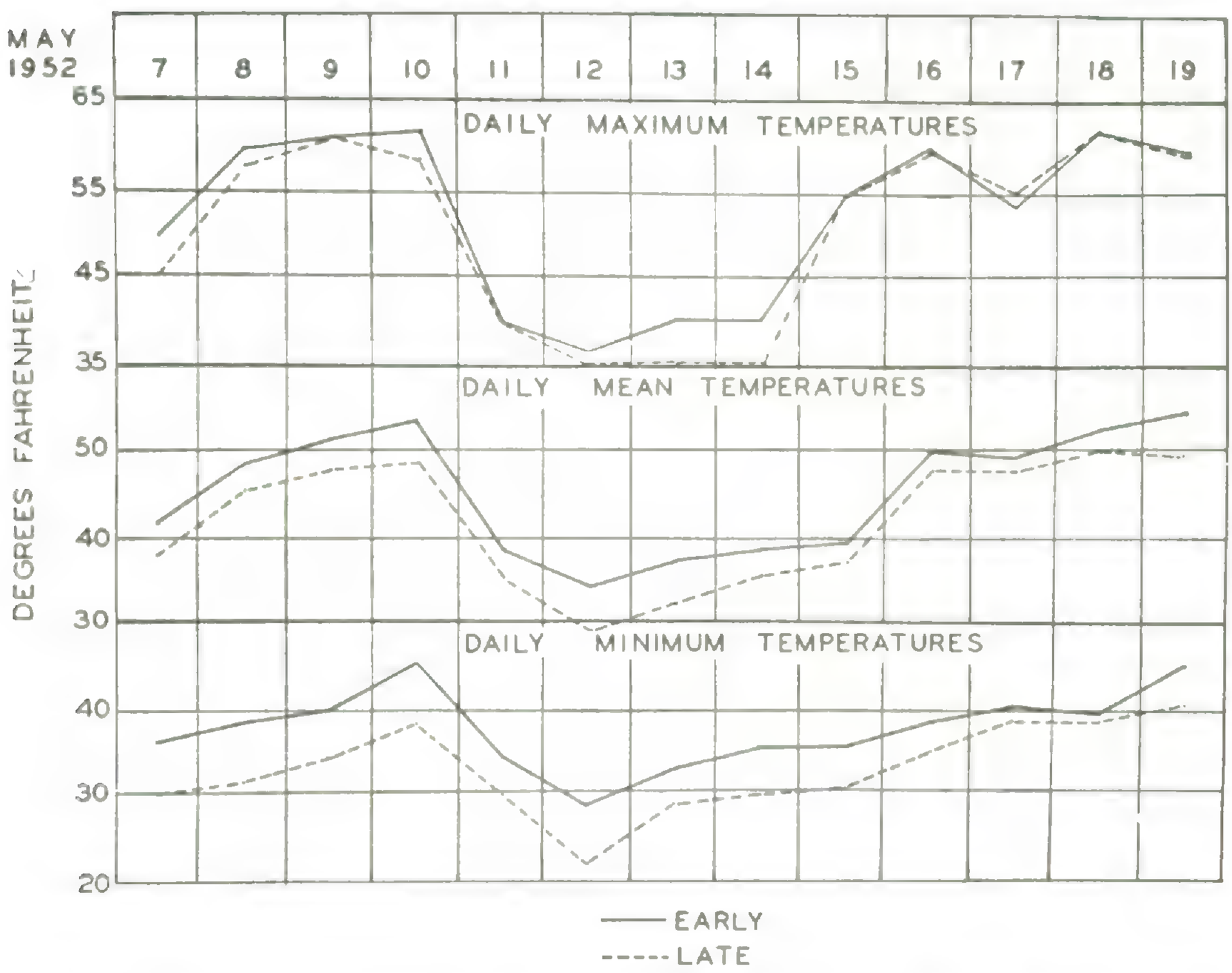

FIG. I. Temperature phenomena of adjacent stands of early- and late-leafing aspen, Stansbury Mountains, Utah. Solid lines early. Broken lines late.

conspicuous differences in leafing time. Figure II represents weekly summaries of the averages of temperature data for two stations each in a pair of contrasting colonies selected for their apparent uniformity of soil and topographical features. Intermittent data from two other pairs of contrasting colonies were also secured throughout the summer. These confirmed the results shown in Figure II.

The data in Figure II reveal that the maximum weekly temperature averaged slightly higher and the minimum temperature averaged slightly lower in the late-leafing colony than in the early-leafing stand, although the mean weekly temperature averages were essentially similar in both. These slight temperature differences may be accounted for by the fact that the late-leafing stand, being slightly more open than the early-leafing colony, allows more sun on the tents by day as well as more effective air circulation by night. However, no aspect of these temperature phenomena is sufficient to account for the great discrepancy of leafing time for these colonies, and the conclusion seems justified that the cause of prevernal leafing lies outside of environmental controls.

FIGURE II

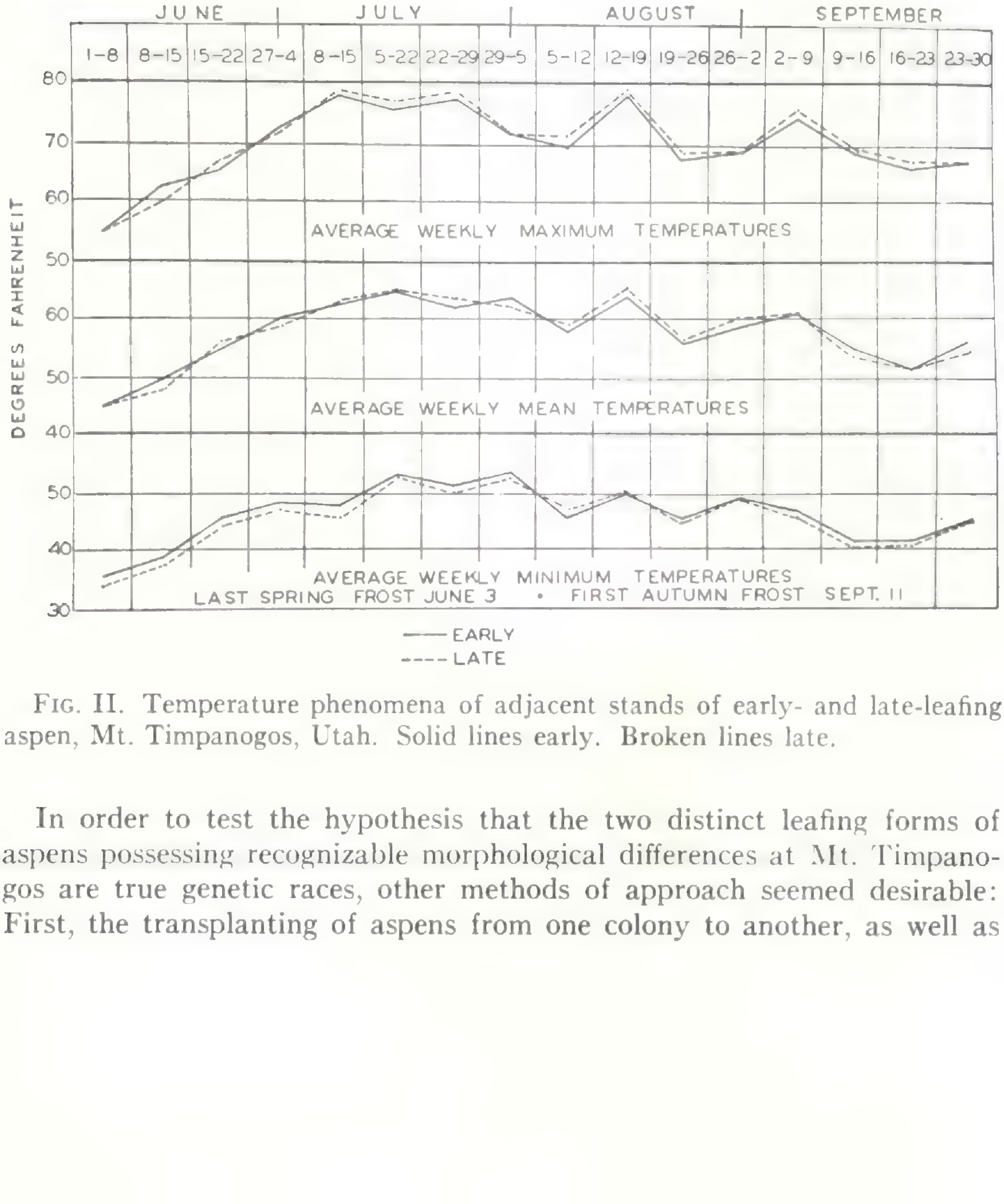

FIG. II. Temperature phenomena of adjacent stands of early- and late-leafing aspen, Mt. Timpanogos, Utah. Solid lines early. Broken lines late.

In order to test the hypothesis that the two distinct leafing forms of aspens possessing recognizable morphological differences at Mt. Timpanogos are true genetic races, other methods of approach seemed desirable: First, the transplanting of aspens from one colony to another, as well as

to a common habitat; second, investigations on the clonal features of the aspen; and third, cytological studies.

TRANSPLANTING EXPERIMENTS

Eight aspen sprouts from three separate pairs of colonies were transplanted in the fall of 1951, thereby introducing into prevernal colonies twelve late-leafing saplings and into late-leafing colonies an equal number of early-leafing saplings. Despite the fact that care was exercised to locate the transplants on the edge of the colonies where competition for light and moisture could be reduced to a minimum, none of the aspen sprouts survived the winter and summer of 1952.

In this experiment it was recognized that several years must elapse before conclusive results might be expected, assuming successful transplantings were possible, because observations have disclosed the fact that aspen sprouts must attain considerable height before they acquire either the morphological characters or the leafing peculiarities of the mature stand. The retarding of the leafing time of the sprouts in prevernal colonies is especially noticeable and may be accounted for by the fact that leafing of the mature trees is generally well advanced before the snow pack has disappeared from the stand. Obviously the close proximity of the snow to the sapling buds has a retarding effect on leafing.

In addition to these transplantings in the field, four saplings from late-leafing aspen stands and four saplings from early-leafing colonies were removed to the University of Utah campus, where previous transplantings of aspen sprouts have proved successful. These transplants were made in late May, 1952, to a favorable situation where nearly uniform factors of soil, water and light were maintained for all saplings.

Three saplings from the late-leafing variety and two from the early survived the summer of 1952 and the winter of 1953. In the spring of 1953 both early-leafing sprouts came into leaf more than two weeks before the late-leafing transplants. Thus the leafing character of the two mountain strains was maintained under totally different environment, and the hypothesis of genetic controls received considerable support.

CLONAL CONNECTIONS OF ASPEN COLONIES

It was assumed that if the present strains of aspen had their origin in seed mutation, contiguous colonies of early- and late-leafing forms should show no clonal connections, although such connections might be expected to exist between trees within the same colony. To determine the nature and extent of aspen clonal connections, at Mt. Timpanogos radioactive phosphorus was employed.*

Selected for radioactive phosphorus treatment was a white-boled, late-leafing tree which occupied a position between closely contiguous colonies of distinct strains of aspen. On one side the branches of this tree inter-

* The writer is indebted to the Research Committee, University of Utah, for supplying the necessary radioactive phosphorus used in this experiment; to Dr. Robert C. Pendleton for labeling the tree; and to Dr. John D. Spikes for monitoring the laboratory specimens.

mingled with those of early-leafing trees and on the other with branches of late-leafing individuals. The nearest bole of the late-leafing variety was 7 feet 6 inches distant, and the nearest bole of the early variety was 6 feet 6 inches. There were six early-leafing trees and seven late-leafing ones within a radius of 17 feet. Near the tree selected for labeling, a trench was excavated exposing the roots, one of which was severed about three feet from the bole. The cut end of this root was inserted into a gallon jar of water containing 40 millicuries of radioactive phosphorus (P–32).

Within 36 hours most of the radioactive phosphorus solution had been absorbed by the tree. The tube of a Geiger counter was placed in a rectangular hole cut breast high in the bark of the labeled tree, thereby exposing the cambium. The counter showed a radioactivity of 60,000 counts per minute. No other tree of either variety in the vicinity of the labeled tree showed radioactivity above background. In subsequent days portions of the roots, cambium, wood and leaves of the labeled tree and of the early- and late-leafing trees surrounding it were removed to the laboratory. These specimens were ashed and tested with a standard scaler provided with a thin-end, window Geiger tube. All ashed samples from the labeled tree gave more than 50,000 counts per minute. No radioactivity above background was found in the samples of any other tree. Excavations around the labeled tree showed that all roots belonging to the labeled tree were radioactive, but that the radioactive substance had not passed to the roots of neighboring trees of either strain.

The results of this experiment are indeed surprising, for they suggest complete separation of the aspen sprouts from the parent clone before or soon after maturity. Considerably more investigation is necessary to establish the clonal characteristics of the aspen.

CYTOLOGICAL TESTS

The field of cytogenetics should offer an interesting and possibly a fruitful approach to the problem of the leafing strains of aspen. So far, however, the writer has encountered perplexing delays in securing suitable tissue for study. Because of the unreliability of aspen seed production, and the major difficulties of securing pollen smears from the remote and snow-bound experimental area, it was assumed that cuttings would provide the most feasible source for securing tissue in active cell division. Numerous greenhouse attempts have been made to root aspen cuttings without a single positive result to date. Additional effort to secure root tips for study is currently in progress.

Positive miscroscopic evidence of chromosome aberrations would, of course, establish the validity of these genetic strains, but negative evidence would not necessarily preclude it, for mutations may be the result of one or a few unobservable gene changes.

DISCUSSION

Whether cytologically demonstrable or not, the fact or the assumption that these readily distinguishable forms of early- and late-leafing aspen

represent mutant strains presents problems of origin and subsequent distribution both interesting and perplexing to the ecologist. For no fact of aspen ecology, in Utah at least, seems more certain than that aspen trees in general, despite occasional abundant viable seed production, reproduce only through vegetative means. They do this because aspen seeds must germinate within a few weeks after ripening in early June. Under present climatic conditions precipitation in Utah is invariably scant and irregular during the summer months. Thus the wide and spotty distribution of aspen throughout Utah today must have been attained under climatic patterns of more abundant and more evenly distributed summer precipitation. Such conditions are postulated by geologists for the Great Basin region during the pluvials associated with the extensive Pleistocene glaciations (1, 2 & 3).

After the onset of the Postpluvial climate in the Great Basin area, which Antevs estimates at approximately 8,000 years ago, it is likely that aspen ceased its reproduction by seeds. Since then migration has been through clonal reproduction only, and exceedingly slow, but sufficient to effect the mergence of many previously separated colonies and to extend the upper altitudinal limits of the aspen belt. Conversely, the increased temperature and lower summer precipitation of the Postpluvial may have caused considerable retreating migration from lower limits of the Pluvial aspen distribution. There are examples of the complete disappearance of aspen colonies at lower elevations during historical times, but grazing influence may have been a contributing cause.

Any proposed hypothesis to explain the origin and present-day distribution of early- and late-leafing aspens must account for the following facts:

1. The predominance of late-leafing forms at low and mid-elevations.
2. The predominance of early-leafing aspen at higher elevations.
3. The widely intermingled colonies of the two forms at mid-elevations, their sharp discontinuity and the purity of their stands.

Assuming that mutations have occurred within the sex cells and therefore have involved successful seedling establishment, it must follow that the mutant strains date back to Pluvial times. Since the altitudinal migration of aspen in Postpluvial times has been mainly upward, and since the late-leafing strain dominates the lower aspen elevations today, the late-leafing form must be the parent type.

It seems obvious that a longer photosynthetic period (upwards of three weeks) acquired by the mutant strains would give them distinct physiological survival advantages over the parent form, particularly at higher elevations where the frost-free period is short, provided, of course, that they also possessed adaptive resistance to lower temperatures. The ability of the early-leafing form to withstand frost in spring is apparent because banks of snow are frequently present beneath the aspen canopy when these trees come into leaf. Temperature records in the early-leafing experimental colony at Mt. Timpanogos, with no snow on the ground in 1951, showed night temperatures of 30° F. or below for a period of approximately

nine hours duration each for June 1, 2 and 3. On the night of June 1, 1951, the minimal temperature of 26° F. prevailed for approximately three hours. The aspen leaves in the early-leafing colony at this time were about one half mature size, while the adjacent late-leafing trees were still in the bud stage.

Whether or not this insensitivity to mild freezing temperature is merely another expression of the same mutation that produced early leafing would be difficult to determine, but certainly the prevernal appearance of aspen leaves would be impossible without this adaptation. That the same degree of frost resistance is not possessed by the late-leafing form is suggested by its apparent inability to invade the upper limits of the aspen belt, by its failure to produce leaves at mid-elevations until the frost period is over and by its habit of dropping leaves earlier in the fall than the early-leafing varieties growing in similar habitats.

At mid-elevations it is apparent that both strains of aspen successfully established seedlings at the close of Pluvial times after these mountain areas had been cleared of the receding ice. It is probable that at lower elevations, high temperature and drought were more limiting as factors of successful aspen establishment than a longer photosynthetic period. Also, suitable sites for aspen were already occupied by the late-leafing parent type. Assuming that neither strain had significant advantage at mid-elevations, the preponderance of seed of the late-leafing strain would account for the dominance of the late-leafing form at mid-elevations today. Clonal reproduction over the centuries of Postpluvial time from trees of these two strains as loci for vegetative migration has, in many instances, brought about the mergence of these two contrasting leafing forms into a single forest stand.

A critical test of this hypothesis awaited the experiment using radioactive phosphorus to trace the clonal relationship of the two strains. It was postulated that a solution of radioactive phosphorus applied to the roots of an aspen of either strain, situated at the line of contact of the diverse colonies, should, according to the hypothesis, pass freely through the root connections to neighboring trees of its own strain, but never to the trees of the opposite strain regardless of their proximity to the labeled tree. The one experiment performed thus far is therefore disappointing as evidence for or against the hypothesis in that it suggests that mature aspen trees in a colony sever their clonal connections.

SUMMARY

1. Almost any aspen forest in early spring in Utah and neighboring states shows sharply discontinuous colonies of trees that attain full leaf two to three weeks earlier than the major stand that surrounds them. The colonies of prevernal aspen are usually small in comparison with the forest as a whole, and in general they are most pronounced at mid-elevations of the aspen belt.

2. Extensive data secured with recording thermographs show that one segment of an aspen forest exhibiting prevernal leafing, is a response to

temperature controls, but that in general the early-leafing colonies of aspen represent distinct genetic strains in which temperature is not a factor.

3. As a rule the leafing habit of the various aspen strains is associated with morphological characters by which they may be identified at all seasons.

4. Saplings of early- and late-leafing strains of aspen transplanted to the University of Utah campus at an elevation of 4,500 feet exhibited the same time difference in leafing as their parent colonies at 7,800 feet.

5. An hypothesis proposed to explain the origin, present distribution and nature of prevernal aspen colonies postulated the following:

(a) Sexual mutations of the late-leafing parent type occurred in Pluvial times.

(b) Migration to and establishment of these strains at higher elevations followed the disappearance of mountain ice and snow packs.

(c) Early-leafing forms dominate the upper limits of the aspen belt because of their longer photosynthetic period and their physiological adaptations to lower temperatures.

(d) Clonal reproduction over the centuries of Postglacial time from seed-established trees as loci for vegetative migration has produced the mergence of these contrasting leafing strains into single forest stands.

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EXPLANATION OF PLATES

PLATE I

Typical stands of early- and late-leafing aspens, mid-elevation (7800 feet). Mt. Timpanogos, Utah. In the right mid-ground is seen the protective tent covering for one of the recording thermographs used to compare atmospheric temperature phenomena of the contiguous aspen strains.

PLATE II

Late-leafing aspens (foreground) have white, well-pruned boles in northern Utah, while the early-leafing forms (background) are yellow-boled and poorly pruned.

Prevernal Leafing of Aspen in Utah Mountains

PREVERNAL LEAFING OF ASPEN IN UTAH MOUNTAINS

THE CONTROL OF TREE GROWTH BY PHLOEM BLOCKS

KARL SAX

With one plate

THE NATURE OF SAP MOVEMENT, nutrient transport and stem polarity in plants has long been known. Thomas Andrew Knight reporting in the Transactions of the Horticultural Society of London in 1822 observed that "the vessels of plants are not equally well calculated to carry their contents in opposite directions" and that "the true sap of trees is wholly generated in the leaves, from which it descends through their bark to the extremities of their roots, depositing in its course the matter which is successively added to the tree." Thus Knight recognized polarity in the transport of elaborated nutrients down the phloem based upon his experiments with inverted cuttings and the effect of girdling the bark of fruit trees. He observed that "it had long been known to gardeners, that taking off a portion of bark round the branch of a fruit-tree occasions the production of much blossom on every part of that branch in the succeeding season." He concluded that the effect of dwarfing stocks in promoting early fruiting and restricting tree growth was similar in nature to the effect of girdling the bark and attributed both effects to the "obstruction of the descending sap."

Phloem blocks induced by killing the stem with steam were used by Dixon (8) and others in their studies on the ascent of sap. The fact that the sap passed up the xylem of the dead stem provided evidence for the "mechanistic" rather than the "vitalistic" theory of the ascent of sap. More recently it has been shown that phloem blocks, induced by killing a section of the stem with heat, prevent the downward movement of vitamins, organic carbohydrates and growth-regulators (Crafts 1951). Bonner (4) girdled the stems of tomato plants with a jet of superheated steam which killed all living tissue. In a few days he found an accumulation of thiamin, pyridoxine, pantothenic acid, riboflavin, sucrose and nitrogen above the girdle. Rabideau and Burr (11) killed sections of bean stems with hot wax and used radioactive carbon to trace the flow of photosynthetic products down the stem. Most of the elaborated organic material accumulated at the dead segment. A phloem block in *Phaseolus* also checked the movement of growth-regulators such as 2,4-D as shown by Weintraub and Brown (15).

It is, however, unnecessary to kill a segment of the stem in order to induce a phloem block. Christensen (5) found that irradiation of a stem segment with X-rays was followed by a swelling of the stem above the irradiated section, and after four or five weeks the swollen area developed roots if the stems were kept moist. The minimum dosage required for such a response was 1500 r for *Xanthium*. Similar results were obtained

with *Nicotiana* at 6000 r, *Lycopersicum* at 24,000 r, and *Phaseolus* at 16,000 r, but the minimum dosage required to induce a response was not determined in these genera. The phloem block induced by irradiation checked the flow of organic materials and auxin down the phloem without killing the stem segment.

It is also possible to impose a phloem block without killing the stem by inverting the scion or by inverting a ring of bark. This technique is based upon the polarity of phloem transport. The botanical studies of stem polarity date back to the work of Vöctung and Sachs with their description of "root-pole" and "shoot-pole." The role of polarity in grafting was probably known by horticulturists for hundreds of years. It was described by the botanist Strasburger (14) as follows — "Unlike poles of a plant may readily be induced to grow together, while like poles may only be brought to do so with difficulty and then do not develop vigorously." This conclusion has been confirmed repeatedly. The inversion of the rootstock has, however, been used to stimulate rooting at the base of the scion in order to get varieties of apple trees on their own roots. Kerr (10) found that such an inverted graft would survive long enough to permit scion rooting above the graft union, due presumably to the accumulation of auxin at the junction of the "root-poles" of stock and scion.

The induction of a phloem block by inverting a ring of bark was reported in 1935, but it is probable that it was also used by the early horticulturists of Europe. According to Roberts (12) the inverted rings checked the growth of the tree, but without the deleterious effect resulting from girdling. Apparently this work was not continued by Roberts.

It is also known that certain incompatible combinations of stock and scion check tree growth as a result of a phloem block induced by an imperfect graft union (2). In some cases, however, the graft union appears to be normal yet there is considerable overgrowth of the scion accompanied by dwarfed growth and precocious fruiting. In these cases perhaps the stem of the scion can utilize the organic carbohydrates from its leaves more effectively than can the stem of the rootstock.

There is some evidence that the dwarfing effect of certain Malling apple rootstocks may be due to a retardation of phloem transport. Dr. F. R. Tubbs, Director of the East Malling Research Station, writes that: "We do not know of any dwarfing apple rootstock that does not induce the formation of a bulge" (personal communication). This swelling of the stem of the rootstock or the section of the interstock could be attributed to the retardation of the downward flow of elaborated organic nutrients and growth stimulants, as suggested by Knight, thus promoting more rapid growth of the Malling rootstock or interstock stem. The fact that a long dwarfing interstock is more effective than a short one, and that certain rootstocks are more dwarfing if budded high on the stem than if budded near the ground, would seem to support the above interpretation (13).

It is known that the dwarfing effects of certain rootstocks are due to factors other than the blocking or retardation of phloem transport. Colby (6) has suggested that the extreme dwarfing effect of the Malling IX

apple rootstock may be due to early suberization of the young roots. There is also evidence that growth can be suppressed, quite independently of the nature of the graft union, by an interaction between the scion variety and the root system of the stock (Sax, Proc. Am. Soc. Hort. Sci., in press).

During the past five years a study of the effect of inverting rings of bark has provided some information on the mechanism of phloem transport and has provided another method for dwarfing fruit and ornamental trees. We began with the inversion of a single ring of bark about an inch long on the stems of one- and two-year-old apple trees. The cuts through the bark were made as parallel as possible, sometimes by using a double bladed knife — in other cases by using a strip of metal tape as a guide. The bark was removed, inverted and wrapped tightly with a rubber band, until the bark had healed onto the stem — a period of a week or ten days.

The inverted bark made little or no growth, but there was a swelling of the stem above the inverted bark and to a lesser extent at the upper edge of the inverted section of bark. At the vertical seam of the inverted ring there was regeneration of tissue and after several months this area had made considerable growth, and after several years it had so dominated the inverted area that the dwarfing effect was largely lost. Apparently there is normal polarity of phloem transport in this regenerated area and it grows rapidly.

In order to effect a more permanent phloem block it was necessary to invert two rings of bark, one directly above the other, and orient the vertical seams on opposite sides of the stem. There is some phloem regeneration at the seams, but any downward transport through the seam of the upper inverted ring is checked when it reaches the intact edge of the lower inverted ring with its vertical seam on the opposite side. A Cortland apple whip was treated in this way five years ago. It has made almost no growth in trunk diameter and has increased in height only about six inches during the past five years, but it has borne several fruits during each of the past two years and appears to be healthy.

In 1953, a group of Baldwin apple trees, budded on a semi-dwarfing rootstock, were used for a bark inversion test. A single ring of bark was inverted on eight two-year-old trees, and above the vertical seam a square of bark was inverted to prevent transport down the regenerated tissue. In the eight controls a ring of bark was removed and replaced in the normal position. In both the bark inversion series and in the controls there was some early sucker growth below the rings, and the first growth of suckers were removed. Subsequent sucker growth was limited almost entirely to the trees with inverted bark. At the end of the growing season the trunk diameter below the bark ring was measured, together with tree height and total length of the branches developed below the inverted bark rings. The results are shown in Table 1, and photographs of a control and of an inverted bark tree are shown in Figures 1 and 2.

The data show that the inversion of the ring of bark reduced the growth of the trees both in trunk diameter and in height. It also promoted the growth of buds below the phloem block, indicating that the auxins

which normally suppress bud development at the base of the trunk had not passed through the inverted ring of bark in sufficient quantities to suppress bud growth. Most of the trees with the inverted bark have flower buds while no flower buds were observed on the control trees. The inverted bark remains alive, so far as can be determined by its appearance, yet growth is suppressed and earlier fruiting is induced.

TABLE 1.

EFFECT OF BARK INVERSION ON TREE GROWTH

Baldwin/524/sikkimensis.

Bark inverted June 1, '53. Measured Oct. 6, '53.

8 Controls			8 Inverted		
Trunk Caliper cm.	Height Feet	Sucker Growth ft.	Trunk Caliper cm.	Height Feet	Sucker Growth ft.
2.0	4.5	0	1.5	3.8	4.1
1.7	5.1	0	1.1	3.1	4.2
1.9	4.6	0	1.4	3.2	4.5
2.1	4.9	0	1.4	3.2	5.1
1.9	4.5	0	1.4	3.1	4.9
1.9	4.0	0	1.6	3.5	2.1
1.6	4.2	0.5	1.5	3.5	3.2
2.1	4.1	0	1.5	3.6	4.7
Ave. 1.9	4.5	−0.1	1.4	3.4	4.1

It should be possible to modify the bark inversion phloem block to permit the desired amount of growth of the tree. A method developed several years ago appears to meet this need. Baldwin two-year-old trees, budded on *Malus sikkimensis* rootstocks, were used. Two bark inversions were made with eight-inch strips of normal bark on opposite sides of the trunk, and the inverted rings were separated by a short segment of normal bark of half an inch to one inch in length. The downward movement through the phloem was limited to the slender strip of normally oriented bark. After passing down the first ring the flow must pass laterally before it can pass down the normal strip of bark in the second ring. Although lateral phloem transport is restricted some material does get through as is evident from the growth shown in Figure 4. It is probable that a short section of normal bark between the inverted rings would have a greater restriction on phloem transport than a long one, so that the degree of dwarfing could be regulated to some extent by varying the length of the central segment between the inverted rings. Thus by adjusting the width of the normal strips of bark in the inverted rings and by varying the length of the normal central segment, it should be possible to obtain any desired degree of dwarfing.

All of these treated trees flowered and several bore fruit the following

year. One of these trees, bearing abundant flower buds as it begins its fourth season's growth, is shown in Figure 3. The details of the double bark inversion are shown in Figure 4. The growth of the normally polarized strips of bark in the inverted rings may eventually result in a direct line of phloem transport through the normal ring of bark between the inverted segments, and the dwarfing effect will be reduced and finally lost. In order to maintain a permanent dwarfing effect the inverted bark technique may have to be repeated, but when a tree reaches the desired size a double inversion with only a very narrow ring of bark (or none at all) between the inverted rings, should insure permanent dwarfing. Since the bark inversion may have to be repeated, this technique for dwarfing trees is not likely to be of much value to the commercial nurseryman. The average back yard horticulturist should, however, have no trouble in using this technique.

In a few cases we have put double upside-down adjacent rings on larger trees (up to 6 inches in diameter) with the hope that further growth could be checked almost completely and yet permit flowering and fruiting. These trees have been treated only for one growing season, and at least several years must elapse before we can recommend such a procedure.

The inactivation of the phloem by ionizing radiation is comparable in several respects to the effects of inverting a ring of bark. The phloem block is induced without killing the bark, swelling of the stem occurs above the treated area and bud growth is stimulated below the phloem block just as it is by inverting the bark. On July 27 the stems of a clonal line of young poplar trees were irradiated with 2,500, 5,000 and 10,000 roentgen units of X-rays respectively. A lead plate with a 1.5 inch slit was placed over the stems to limit the radiation to the short stem segment. After several weeks the swelling above the irradiated areas became evident particularly at the higher doses. On Oct. 6th the six trees receiving 2500 or 5000 r were all alive, but at 10,000 r four of five treated trees were dead above, at, and for some distance below the irradiated segment. This higher dosage may have killed the tissue completely, followed by the separation of the bark from the xylem as a result of the overgrowth of the stem above the irradiated area, as shown in Figure 3. The inverted bark produced a similar overgrowth, but without pulling the bark from the stem in the treated segment. At the lower doses of X-rays there was evidence of a phloem block with no death of the stem at the irradiated area.

It is evident that it is possible to produce a phloem block without killing the stem by inverting a ring of bark or by non-lethal exposure of a stem segment to X-rays. In both cases the growth of the treated area is restricted or suppressed. The suppression of growth may be the cause of the phloem block in these cases. According to Abbe and Crafts (1) —"It is characteristic of the sieve tubes of all plants, that, after a brief functioning period — consisting of from a few days in the case of protophloem sieve tubes to a single season in most woody plants — the elements collapse, and death occurs."

The X-ray induction of a phloem block without killing the tissue is apparently due to nuclear injury which prevents continued cell division without killing the cytoplasm. It is known that the cytoplasm is very much more resistant to injury from X-rays than is the nucleus. Thus the sieve tubes already formed could continue to function, but no new ones would be formed to augment and replace those present at the time of irradiation.

The bark inversion also seems to produce a phloem block by the inhibition of cell division. The suppression of growth in the inverted bark rings is apparently due to the inability of nutrients and auxins to move freely against the reversed polarity. There is usually a slight swelling of the top of the inverted bark ring, indicating some diffusion of nutrients, but there is little or no growth of the inverted segment as a whole. Thus the inversion of the bark may check growth by the failure of nutrients to move freely through the inverted phloem tissue.

The new phloem produced at the vertical seam in inverted bark segments appears to be normally polarized since this tissue grows rapidly. Any new phloem tissue produced within the inverted ring of bark should eventually also be normally polarized, but the fact that growth does not occur indicates that few or no sieve tubes are produced, presumably due to the checking of nutrient flow through the inverted segment. The fact that bark inversions made early in the growing season do not survive as well as those made in June and August suggests that some active sieve tubes are needed even though the inverted polarity checks the passage of nutrients and auxins down the stem. Since a tree has lived for five years with a double inverted ring of bark, some material must be transmitted either through the inverted bark or through some other part of the stem.

SUMMARY

A phloem block can be induced without killing the stem tissues by exposing stem segments to X-rays sufficient to suppress cell division or by inverting a ring of bark. The phloem block induced by irradiation appears to be due to the failure of renewal of phloem elements. The reversed polarity of the inverted ring of bark also prevents renewal of phloem elements, presumably by preventing the adequate movement of nutrients and auxins into the inverted phloem cells. The inversion of rings of bark may be modified to produce the degree of dwarfing desired in fruit and ornamental trees.

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DESCRIPTION OF FIGURES

FIG. 1. Baldwin tree, 2 years old, on semi-dwarfing rootstock. A ring of bark was removed and replaced in the normal position on June 1, 1953. This control tree has made considerable growth in a single season.

FIG. 2. Baldwin tree, 2 years old, on semi-dwarfing rootstock. A ring of bark was inverted June 1, 1953. Note dwarfing effect in a single season, and the production of flower buds. The suckering below the inverted ring of bark indicates the checking of auxin flow.

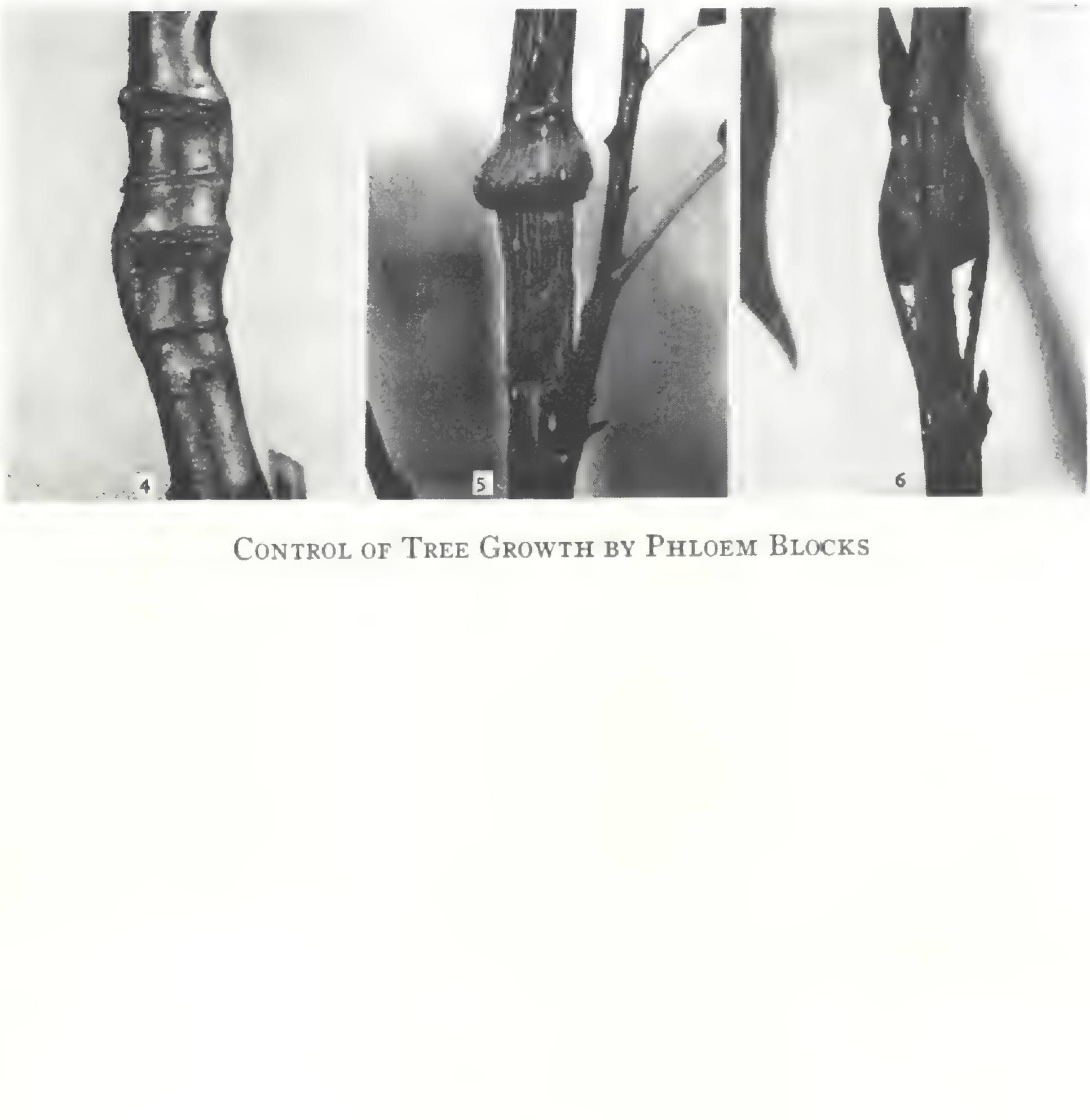
FIG. 3. Baldwin on *M. sikkimensis*, 3 years old, dwarfed by double inverted ring with a slender strip of normal bark on the opposite side of each of the two inverted rings. A short section of normal bark was left between the two inverted rings. This tree bore fruit in its third growing season and bears many flower buds as it begins its fourth year.

FIG. 4. Details of double bark inversion show how phloem transport is checked. The swelling of the upper end of the inverted ring of bark suggests some nutrients and auxins may flow into the inverted bark by diffusion, but active phloem transport is blocked by the reversed polarity of the inverted phloem tissue.

FIG. 5. A poplar stem with inverted ring of bark, showing swelling of the stem above the phloem block imposed by reversed polarity of the phloem.

FIG. 6. A poplar stem exposed to 10,000 r of X-rays. Note the similar swelling of the stem above, and the suckering below, of the irradiated section of stem. The X-rays impose a phloem block by preventing cell division and the renewal of phloem cells. In this case the bark was killed and is pulled away from the wood by the expansion of the stem above the irradiated area, but it is possible to impose a phloem block with X-rays without killing the tissue.

Photographs by Heman Howard.



CONTROL OF TREE GROWTH BY PHLOEM BLOCKS

CRYPTOGAMS OF THE 1948 ARCHBOLD CAPE YORK (QUEENSLAND) EXPEDITION

P. BIBBY

MUSCI *

LEMBOPHYLLACEAE

Camptochaete brisbanica (C. M.) Broth., Proc. Linn. Soc. N. S. W. 43: 561. 1916.

QUEENSLAND: Mt. Finnegan, *Brass 20058, 20155*, Sept. 1948, alt. 850 m., on branches in rain-forest undergrowth; Mossman River Gorge, *Brass 18173*, Mar. 1948, alt. 150 m., plentiful on granite rocks in rain-forest.

Not compared with the type, but agreeing well with material so named in the National Herbarium of Victoria.

HOOKERIACEAE

Eriopus sp. (aff. *E. apiculatus* [Hk. f. & W.] Mitt.).

QUEENSLAND: Mt. Finnegan, *Brass 20097*, Sept. 1948, alt. 1040 m., trunk of a tree in high mountain forest.

Very close to and probably identical with *E. apiculatus* (Hk. f. & W.) Mitt.

HEPATICAE

PTILIDIACEAE

Mastigophora Nees

Mastigophora diclados (Endl.) Steph., Spec. Hep. 4: 38. 1909.

QUEENSLAND: Leo Creek, Upper Nesbit River, *Brass 19957*, Aug. 1948, alt. 420 m., cushioned on trees on bank of creek in rain-forest.

LEPIDOZIACEAE

Bazzania S. F. Gray

Bazzania adnexa (L. & L.) Mont., Voy. au Pole Sud. 243. 1842–45.

QUEENSLAND: Lamb's Head, Lamb Range, *Brass 18227*, Mar. 1948, alt. 1000–1100 m., sunny rocks in rain-forest; Mt. Bellenden-Ker, summit of south peak, *Brass 18288*, Apr. 1948, alt. 1550 m., on trees of low forest.

Bazzania Novae-Zelandiae (Mitt.) Kuntze, Gen. Plant. 832. 1901.

* Determined by J. H. Willis.

QUEENSLAND: Mt. Finnegan, *Brass 20144*, Sept. 1948, alt. 1140 m., on bark of a tree in high mountain scrub.

Lepidozia Dumort.

Lepidozia capilligera (Schwaegr.) Lindenb., Syn. Hep. 204. 1844.

QUEENSLAND: Iron Range, *Brass 19051*, June 1948, alt. 20 m., on a decaying log in floodplain in rain-forest.

HARPANTHACEAE

Chiloscyphus Corda

Chiloscyphus argutus (R. B. & N.) Nees, Syn. Hep. 183. 1845.

QUEENSLAND: Iron Range, *Brass 19052*, June 1948, alt. 20 m., on decaying logs in floodplain rain-forest.

JUNGERMANNIACEAE

Anastrophyllum (Spruce) Steph.

Anastrophyllum piligerum (Nees) Spruce, Jour. Bot. **14**: 33. 1876.

QUEENSLAND: Mt. Bellenden-Ker, summit of south peak, *Brass 18286*, Apr. 1948, alt. 1550 m., abundant on trees of low forest.

Chandonanthus Mitt.

Chandonanthus hirtellus (Web.) Steph., Spec. Hep. 3: 643. 1909.

QUEENSLAND: Mt. Bellenden-Ker, summit of south peak, *Brass 18285*, Apr. 1948, alt. 1550 m., on a tree in low forest.

PLAGIOCHILACEAE

Plagiochila Dumort.

Plagiochila abietine * (Nees.) Lindenb., Mon. Hep. Gen. Plag. 134. 1844.

QUEENSLAND: Mt. Finnegan, *Brass 20141*, Sept. 1948, alt. 1140 m., shrubberies of the summit.

This constitutes the first record of this species on the Australian mainland.

Plagiochilon Hattori

Plagiochilon oppositus (R. B. & N.) Hattori, Biosphaera 1: 7. 1947.

Plagiochila opposita (R. B. & N.) Dum., Rec. d'obs. 15. 1835.

QUEENSLAND: Mt. Finnegan, growing with *Sticta*, *Brass 20095*, Sept. 1948, alt. 1100 m., on mossy rocks in high mountain.

Not previously reported on the Australian mainland.

* Determined by Th. Herzog, Jena.

SCHISTOCHILACEAE

Schistochila Dumort.

Schistochila cristata Steph., Hedw. **28**: 274. 1889.

QUEENSLAND: Mt. Finnegan, *Brass 20089*, Sept. 1948, alt. 1100 m., very abundant on rocks (granite) in high mountain forest.

RADULACEAE

Radula Dumort.

Radula acutiloba Steph., Hedw. **28**: 271. 1889.

QUEENSLAND: Leo Creek, Upper Nesbit River, *Brass 19954*, Aug. 1948, alt. 420 m., on dead twigs in rain-forest undergrowth.

Radula buccinifera (Hk. f & Tayl.) Tayl., Syn. Hep. 261. 1845.

QUEENSLAND: Mt. Finnegan, *Brass 20094*, Sept. 1948, alt. 1100 m., on leaves and branchlets of undergrowth in high mountain forest.

Radula reflexa Mont., Ann. Sc. Nat. **19**: 255. 1843.

QUEENSLAND: Mossman River Gorge, *Brass 18177*, Mar. 1948, alt. 150 m., moist shady granite rocks in rain-forest.

PLEUROZIACEAE

Pleurozia Dumort.

Pleurozia articulata (Linb.) Schiffn., Engl. Pflanzenfam. I. 3: 115. 1895.

QUEENSLAND: Mt. Finnegan, *Brass 20142*, Sept. 1948, alt. 1140 m., on living twigs in shrubberies of summit; Mt. Bellenden-Ker, summit of south peak, *Brass 18287*, Apr. 1948, alt. 1550 m., hanging from dead twigs in low forest.

FRULLANIACEAE

Frullania Raddi

Frullania Johnsonii Steph., Hedw. **33**: 163. 1894.

QUEENSLAND: Mt. Bellenden-Ker, summit of south peak, *Brass 18289*, Apr. 1948, alt. 1550 m., on dead twigs.

Frullania sp.

QUEENSLAND: Summit of Mt. Tozer, Tozer Range, *Brass 19497*, July 1948, alt. 540 m., living branches of *Casuarina* in scrub of summit.

LEJEUNEACEAE

Drepanolejeunea (Spruce) Schiffn.

Drepanolejeunea Micholitzii Steph. var. **genuina** Herz. Ann. Bryol. 7: 80. 1934.

QUEENSLAND: Mt. Finnegan, *Brass 20098*, Sept. 1948, alt. 1040 m., on leaves of undergrowth in high mountain forest.

Drepanolejeunea obliqua Steph., Hedw. **35**: 82. 1896.

QUEENSLAND: Mt. Finnegan, associated with *Brass 20144*, Sept. 1948, alt. 1140 m., on bark of a tree in high mountain scrub.

Drepanolejeunea tenuis (Nees) Schiffn., Consp. Hep. Arch. Ind. 280. 1898.

QUEENSLAND: Lamb's Head, Lamb Range, associated with *Brass 18227*, Mar. 1948, alt. 1000–1100 m., sunny rocks in rain-forest.

Physocolea Spruce

Physocolea trichomanis (Gott.) Steph., Spec. Hep. **5**: 912. 1916.

Cololejeunea trichomanis (Gott.) Steph., Hedw. **28**: 168. 1889.

QUEENSLAND: Mt. Finnegan, west slopes, *Brass 20054*, Sept. 1948, alt. 850 m., on leaves of an undergrowth tree in rain-forest.

LICHENES

SPHAEROPHORACEAE

Sphaerophorus Pers.

Sphaerophorus compressus Ach., Meth. Lich. 135. 1803.

QUEENSLAND: Lamb's Head, Lamb Range, *Brass 18234*, Mar. 1948, alt. 950–1000 m., sunny rocks in rain-forest.

COENOGONIACEAE

Coenogonium Ehrenh.

Coenogonium implexum Nyl., Ann. Sc. Nat. **16**: 92. 1861.

QUEENSLAND: Speewah, Upper Clohesy River, *Brass 18209*, Mar. 1948, alt. 450 m., trunk of a tree in rain-forest.

CLADONIACEAE

Cladonia Hill.

Cladonia aggregata (Sw.) Ach., Vet. Acad. Nya Handl. **16**: 68. 1795.

QUEENSLAND: Lamb's Head, Lamb Range, *Brass 18232*, Mar. 1948, alt. 950–1000 m., sunny rocks in rain-forest; summit of Mt. Tozer, Tozer Range, *Brass 19495*, July 1948, alt. 540 m., in shelter of boulders on exposed granite rock faces; Mt. Bellenden-Ker, summit of south peak, *Brass 18290*, April 1948, alt. 1550 m., on peaty ground of a small clearing.

Cladonia verticillata Hoffm. var. **cervicornis** (Ach.) Flot., Linnaea 22: 380. 1849.

QUEENSLAND: Lamb's Head, Lamb Range, *Brass 18233*, Mar. 1948, alt. 950–1000 m., sunny rocks in rain-forest.

PANNARIACEAE

Pannaria Del.

Pannaria myrioloba Muell.-Arg., Bull. d'Herb. Boiss. 4: 92. 1896.

QUEENSLAND: Mt. Bellenden-Ker, summit of south peak, *Brass 18291*, April 1948, alt. 1550 m., on bark of living tree in low forest; Mt. Bellenden-Ker, summit of south peak, *Brass 18292*, April 1948, alt. 1550 m., on dead twigs in low forest.

Pannaria sublurida Nyl., Ann. Sc. Nat. 11: 256. 1859.

QUEENSLAND: Mt. Bellenden-Ker, summit of south peak, *Brass 18293*, April 1948, alt. 1550 m., growing on bryophytes.

COLLEMACEAE

Leptogium S. F. Gray

Leptogium phyllocarpum (Pers.) Mont. var. **isidiosum** Nyl., Syn. Meth. 1: 130. 1858.

QUEENSLAND: Mossman River Gorge, *Brass 18168*, Mar. 1948, alt. 150 m., on rocks on edge of a rain-forest stream.

STICTACEAE

Sticta Schreb.

Sticta aurata Ach., Meth. Lich. 277. 1803.

QUEENSLAND: Mt. Finnegan, *Brass 20359*, Sept. 1948, alt. 910 m., on living bark of an exposed branch in high mountain forest.

Sticta Sayeri Muell.-Arg., Flora 71: 23. 1888.

QUEENSLAND: Lamb's Head, Lamb Range, *Brass 18235*, Mar. 1948, alt. 950–1000 m., sunny rocks in rain-forest.

Sticta sulphurea Schaer., Moritz. Verz. 127. 1846.

QUEENSLAND: Mt. Finnegan, west slopes, *Brass 20059*, Sept. 1948, alt. 850 m., on a rotting log in rain-forest.

Sticta sp.

QUEENSLAND: Mt. Finnegan, *Brass 20095*, Sept. 1948, alt. 1100 m., abundant on mossy rocks in high mountain forest.

PARMELIACEAE

Parmelia Ach.

Parmelia latissima Fee forma **sorediata** Nyl., Syn. Meth. 1: 380. 1858.

QUEENSLAND: Tozer Range, north end, *Brass 19369*, June 1948, alt. 300 m., exposed granite rocks on summit.

HYMENOLICHENES

THELEPHORACEAE

Dictyonema Agardh

Dictyonema irpicinum Mont., Ann. Sc. Nat. **10**: 119. 1848.

QUEENSLAND: Leo Creek, Upper Nesbit River, *Brass 19958*, Aug. 1948, alt. 420 m., on a mossy log in rain-forest.

National Herbarium of Victoria,
South Yarra, Victoria,
Australia.

ADDITIONAL NOTE ON NOTHOFAGUS

C. G. G. J. VAN STEENIS

With one text-figure

THE PAPER on New Caledonian *Nothofagus* by Dr. M. Baumann-Bodenheim alluded to in my revision [1] was preceded by a preliminary note.[2] Also after a personal interview at Leyden, May 12, 1953, when we again interchanged data, Baumann-Bodenheim still cherished the idea that the New Caledonian representatives of *Nothofagus*, as well as some of those from New Guinea, belong to a distinct genus, *Trisyngyne* Baill., on the single evidence that these species should have "branched caducous ♂ inflorescences," though he later admitted these "inflorescences" were short-twigs. The confusion arises through the fact that the leaf-blades at the base of the flush are often reduced and both the ♂ triads and cupules appear clasped between the stipules. Such a lateral twig in flush may give the superficial impression of an "inflorescence." Morphologically it remains a twig with lateral inflorescences. Whether these short twigs fail to develop further into persistent branches is entirely irrelevant. In the New Guinean species the flowering twigs are usually persistent and not caducous. For these reasons I maintain that the five perfectly good species described by Baumann-Bodenheim belong to *Nothofagus* sect. *Calusparasus* subsect. *Bipartitae* series *Triflorae* Steen.

The following transfers are therefore necessary:

Nothofagus

Trisyngyne Baill. Adansonia **11**: 136. 1873, syn. nov.

Nothofagus codonandra (Baill.) comb. nov.

Trisyngyne codonandra Baill. Adans. l.c.; Baumann-Bodenheim, Bull. Mus. Hist. Nat. Paris II. **25**: 420. 1953.

Nothofagus baumanniae (Baum.-Bod.) comb. nov.

Trisyngyne baumanniae Baum.-Bod. l.c. 420.

Nothofagus balansae (Baill.) comb. nov.

Trisyngyne balansae Baill. l.c. 137; Baum.-Bod. l.c. 420.

Nothofagus discoidea (Baum.-Bod.) comb. nov.

Trisyngyne discoidea Baum.-Bod. l.c. 420.

Nothofagus aequilateralis (Baum.-Bod.) comb. nov.

Trisyngyne aequilateralis Baum.-Bod. l.c. 421.

[1] Van Steenis, Jour. Arnold Arb. **34**: 308. 1953.
[2] Baumann-Bodenheim, Bull. Mus. Hist. Nat. Paris II, **25**: 419–421. 1953.

Mainly through the generous assistance of Dr. F. Kausel, Santiago de Chile, I obtained some valuable additional material which enabled me to complete my former paper [1] with some interesting illustrations of the

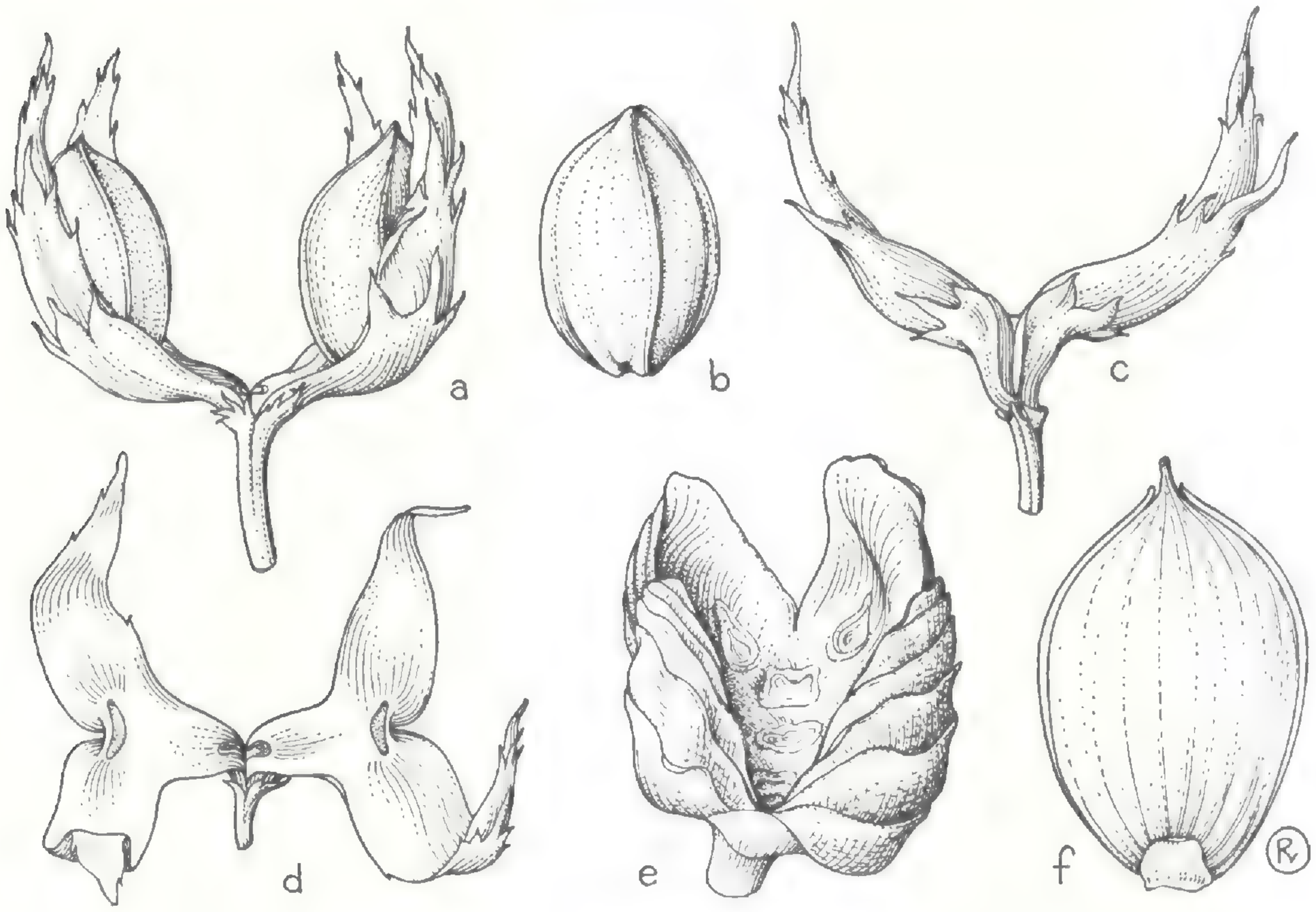


FIGURE 1. *Nothofagus glauca* (Philippi) Krasser. a. Cupule with two lateral nuts, of the central nut only the scar of its attachment is visible. b. A single nut. c. A pair of cupular arms from the exterior showing the sulcate concrescence. d. The cupule without nuts as seen from above, × 1 2/3 (KAUSEL 1319). — *Nothofagus alessandri* Espinosa. e. Cupule seen obliquely from the side, showing the three basal scars and two additional ones at the base of the cupular valves. × 4 (KAUSEL 2303). — *Nothofagus resinosa* Steen. f. Mature nut with reduced cupular valve, × 4 (WOMERSLEY N.G.F. 5134).

cupules of the inadequately known *N. alessandri* Espinosa (fig. 1 e) and *N. glauca* (Phil.) *Krasser* (fig. 4 a–d).

Another interesting figure is that of the mature nut of *N. resinosa* Steen. from New Guinea, for which I have to thank Mr. J. S. Womersley, Lae. This shows that the reduced elamellar cupule of this species is not appreciably enlarged in fruit.

[1] Van Steenis, Jour. Arnold Arb. 34: 308. 1953.

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LEYDEN, THE NETHERLANDS.

NEW ZEALAND CONIFERS

VIVIENNE DELLOW CASSIE

With one plate

ONE OF THE MOST DISTINCTIVE ELEMENTS in the New Zealand flora is that formed by the native conifers, which are to be found in almost every scrub and forest community from North Cape to Stewart Island. They are no longer to be found, however, on the outlying islands. There are twenty species, all endemic, distributed among three families in five genera. In size they range from the pygmy pine (*Dacrydium laxifolium*), the world's smallest conifer, which may bear cones at a height of eight centimeters (cf. Cheeseman 1925), to giant kauris and podocarps well above thirty metres. A height of nearly sixty metres has been reported for kahihatea (*Podocarpus dacrydioides* — Entrican and Reid, 1949).

A detailed discussion of the taxonomic features of each species would be superfluous here, since a number of adequate descriptions are already available. These are located in the works of Kirk (1889), Cheeseman (1925), Allan (1929), Cockayne and Turner (1939), Laing and Blackwell (1940), and Dallimore and Jackson (1948). Instead, the relevant literature will be briefly reviewed, although this account does not pretend in any way to be an exhaustive one.

An anatomical basis for taxonomic studies has been adopted by several workers. Seward and Ford (1906) and Eames (1913) have contributed to the knowledge of the Araucariaceae in general and of *Agathis australis* in particular; Eames from a morphological standpoint, the former authors making a broader phylogenetic approach. An early investigation of leaf anatomy of New Zealand conifers was made by Griffin (1907). More recently, a detailed survey of leaf anatomy in *Podocarpus* has been attempted by Buchholz and Gray (1948), and Gray and Buchholz (1951). These authors place the South Pacific species *P. spicatus* and *P. ferrugineus* in a new subsection (*Euprumnopitys*) of the section *Stachycarpus*. The new subsection, *Euprumnopitys*, is distinguished by the absence of idioblasts (i.e. sclerids) in the mesophyll of leaves. Except for *Podocarpus dacrydioides* in the section *Dacrycarpus*, the remaining New Zealand species fall into subsection D of *Eupodocarpus*, based on the absence of accessory transfusion tissue. Geographic distribution of *Podocarpus* has been studied by Foweraker (1934), and later by Buchholz and Gray (1948). The latter regard the Wegener theory of continental drift as the only feasible solution to distribution problems in this genus. There is some evidence from leaf anatomy that migration between Australia-New Zealand and South-Central America may have taken place in both directions (Buchholz and Gray, op. cit., p. 61). *Eupodocarpus* is regarded as the most advanced section because of the hypostomatic leaves (stomata con-

fined to the under surface), and the usually prominent accessory transfusion tissue. This feature is lacking, however, in subsection D, which contains the New Zealand species. In the section *Stachycarpus*, *Podocarpus spicatus* has the most primitive known arrangement of female cones.

With a view to practical application, Orman and Reid (1941, 1946) have investigated wood anatomy in the genus *Dacrydium*. These workers have constructed a key for the native *Dacrydium* species, using diagnostic features of wood structure. An informative series of bulletins has been published by the New Zealand Forest Service (Ward and Reid, 1949, Entrican and Reid, 1949) on properties and uses of six of the major timber-producing trees in the country (*Dacrydium cupressinum*, *Podocarpus ferrugineus*, *P. spicatus*, *P. totara*, and *Agathis australis*).

Not the least interesting feature of the New Zealand conifers is the prevalence of distinct juvenile leaf forms (Cockayne, 1932). These occur in all species save a few of the podocarps (*P. totara*, *P. hallii*, *P. nivalis* and *P. acutifolius*). Epharmony, too, may cause plants of the same species to have a very dissimilar appearance when grown under different habitat conditions. For example, *Podocarpus nivalis*, a medium-sized bushy shrub in shade and shelter, is reduced to a prostrate shrub with much smaller leaves in direct sunlight (Cockayne, op. cit.).

Hybrids, although not as common as in angiosperm genera like *Hebe* and *Coprosma*, are known or suspected between the following species:*

Podocarpus acutifolius × *nivalis*
Podocarpus hallii × *nivalis*
Podocarpus hallii × *totara* (= *P. loderi* Cockn.)
Podocarpus hallii × *acutifolius*?
Podocarpus ferrugineus × *totara*?
Podocarpus spicatus × *totara*?
Dacrydium bidwillii × *laxifolium*
Dacrydium bidwillii × *biforme*?
Dacrydium biforme × *laxifolium*?
Phyllocladus glaucus × *trichomanoides*?
Libocedrus bidwillii × *plumosa*?

Ecological studies are more restricted in number, centering mainly about the kauri (*Agathis australis*). Cranwell and Moore (1936) drew attention to modified growth forms of kauris growing above a height of 660 metres on Te Moehau (Coromandel Peninsula), a refuge of both alpine and subtropical remnants. Further autecological notes have been made by McKinnon (1937, 1940–41), McKinnon and Dumbleton (1935), Harrison-Smith (1938), and Foley (1950). Recently Mirams (1948, 1951, unpubl.) has analysed in detail the environmental factors responsible for growth and regeneration of the kauri. Root nodules of New Zealand conifers were investigated by Yeats (1924).

An important contribution is that of Cranwell (1940), who has described and figured pollen grains of all the New Zealand species, as well as formulating distinctive generic and specific characters according to the peculiarities of each type of pollen grain. Her work indicates that *Dacrydium bidwillii* and probably also *D. biforme* and *D. kirkii* are rightly

* See Cockayne 1932, Cockayne and Allan 1934, Cockayne and Turner 1939.

placed in a group apart from *Podocarpus*, where Sahni and Mitra (1927) would put them, on the basis of the structure of female cones alone. Cranwell (1938) had previously attempted a partial solution of post-glacial vegetation problems through an analysis of pollen from South Island peat beds. Three main periods are recognised:

1. A grassland period correlated with quite uniformly harsh climatic conditions;

2. A warmer and wetter podocarp period;

3. A mosaic of grassland and beech (*Nothofagus*) forest resulting from local climatic differentiation.

The role played by conifers in New Zealand's past geological time has been clarified still further through the work of Harris, Fergusson and Couper (1951). It appears that a number of extinct species, including at least seven podocarps, dominated forest communities between early Cretaceous and Upper Eocene times. Of the present-day species, *Podocarpus dacrydioides* dates from the Oligocene, and *Phyllocladus* is known even earlier from Upper Cretaceous beds.

CLASSIFICATION

The following is an outline classification of the New Zealand species. A revised key to the species and genera occurring in this country has been published previously (Hay and Dellow, 1952).

Araucariaceae

Agathis Salisb.

Agathis australis Salisb. Kauri

Cupressaceae

Libocedrus Endl.

Libocedrus plumosa (Don) Sargent (= *L. doniana* Endl.) Kawaka
Libocedrus bidwillii Hook. f. Kaikawaka, mountain cedar

Podocarpaceae

Podocarpus L'Hérit.

Section: *Stachycarpus*

Subsection: *Euprumnopitys*

Podocarpus spicatus R. Br. Matai, black-pine
Podocarpus ferrugineus D. Don. Miro, brown-pine

Section: *Dacrycarpus*

Podocarpus dacrydioides A. Rich. (FIG. 1). Kahikatea, white-pine

Section: *Eupodocarpus*

Subsection: *D*

Podocarpus totara D. Don. Totara

Podocarpus hallii T. Kirk. Hall's totara, thin-bark totara
Podocarpus acutifolius T. Kirk
Podocarpus nivalis Hook. Alpine totara

Dacrydium Soland.

Dacrydium cupressinum Soland. Rimu, red-pine
Dacrydium kirkii F. Muell. Monoao
Dacrydium biforme (Hook.) Pilger. Pink-pine
Dacrydium bidwillii Hook. f. Bog-pine, mountain pine
Dacrydium colensoi Hook. Silver-pine
Dacrydium intermedium T. Kirk. Yellow silver-pine
Dacrydium laxifolium Hook. f. Pygmy pine

Phyllocladus L. C. Rich.

Phyllocladus trichomanoides Don. Tanekaha
Phyllocladus glaucus Carr. Toatoa
Phyllocladus alpinus Hook. f. Mountain toatoa

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WELLINGTON, NEW ZEALAND.

PLATE I

Podocarpus dacrydioides A. Rich. growing in beech (*Nothofagus*) forest about 620 metres above sea level, near Lake Waikaremoana, New Zealand.

PODOCARPUS DACRYDIOIDES A. RICH.

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A MONOGRAPH OF THE GENUS PHILADELPHUS

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With six plates

INTRODUCTION

Philadelphus is geographically one of the most widely distributed genera in nature, ecologically one of the most varied groups in habitat, and horticulturally one of the most popular shrubs in our gardens. Its slightly discontinuous distribution forms a belt girdling the temperate zone of the northern hemisphere, extending to the higher altitudes in the tropics in North America. The early inhabitants of Asia Minor, Eastern Asia and Central America, centers where different culture patterns originated, have independently discovered its merits and have brought under cultivation many species for their showy flowers, their enticing fragrance, or for their medicinal value. In ancient times the Parthians employed the flowers in the preparation of hair perfume, and the advanced people of Mexico, and apparently those of Central America, used the flowers for making garlands, and the leaves for medicine. By the early part of the eleventh century, the Chinese garden forms had developed to such a degree of excellence that they were presented by the people of Szechuan as special tributes to the emperor in Peking. Due to their hardiness, their ability to tolerate a wide range of environmental conditions, their ease of propagation, and their flowering late in the spring season, the species of *Philadelphus* have become garden favorites, especially in the northern hemisphere.

By the latter part of the nineteenth century, forms of both Asiatic and American origin were established in various European gardens. Much was written about them, and very many binomials based on these exotic forms were published. Sometimes several or even up to a dozen different names were assigned to specimens taken from plants of the same origin. Some of the individual authors had only limited material for purposes of comparison, and others lacked specimens from the type localities. Thus it was inevitable that specific names were multiplied and much confusion resulted. In addition, clerical errors in recording names and in labeling living plants and preserved material provided further complication. In

some cases proposed new species were accredited to regions remote from their actual place of origin. Naturally different names came into use for species which not even a specialist could distinguish, and at the same time a single name may have been applied to very different species. Both botanists and horticulturists have complained of this nomenclatural confusion, yet since 1896 there has been no monographic work for the clarification of the entire group. Only scattered papers treating selected species or isolated groups from certain areas have been published. Actually, the lack of uniformity in selecting diagnostic characters by different authors has created further confusion. Thus it is that a practical scheme for the classification of the numerous species in the light of modern taxonomic knowledge and under the regulations of the accepted code of nomenclature is an urgent need.

Unaware of the difficulties in identifying species of this genus, I tried to name some unstudied Chinese material in the Arnold Arboretum herbarium. To my surprise, I was unable to find a workable key which could enable me to distinguish the Asiatic forms. After studying all the original descriptions I found myself even more confused for most of them are so meagre and the characters indicated are so generalized that one description often applies to any one of a number of obviously different species. I turned to more experienced taxonomists and horticulturists for advice and was warned that the species of *Philadelphus* have long been a botanical problem, and it would be wise for me to leave them alone. Though inexperienced in the group and perplexed by the confusion, I had the conviction that the man-made disturbances in the classification of the group could be solved when a real knowledge of the plants themselves had been acquired. I thus commenced an intensive study of the genus involving both living and herbarium material. My hope was that by careful examination of a large number of herbarium specimens collected from various centers of the natural range of the species supplemented with firsthand observations on the living plants cultivated in the Arnold Arboretum, the general pattern of the evolution of the genus might be discovered, and a natural order of relationship of the diversified taxa within the genus might be outlined. Besides the material deposited in the herbarium of the Arnold Arboretum (A) and the Gray Herbarium (G) of Harvard University, large loans were obtained from the Bailey Hortorium of Cornell University (BH), the Chicago Natural History Museum (F), the Missouri Botanical Garden (MO), the New York Botanical Garden (NY), the University of Tennessee (TENN), and the United States National Herbarium (US). In September 1952, after the annual meeting of the American Society of Plant Taxonomists which took place at Cornell University, I examined the *Philadelphus* collection of the Wiegand Herbarium of that University (CU) and incorporated the notes in my manuscript. With these specimens, vegetative as well as floral characters were carefully analyzed. One by one the characters of geographically remote yet morphologically close taxa were intensively studied. Variations in each character were plotted with due allowance

for changes that may be caused by the age and vitality of the plant as observed in cultivated forms. The more constant characters were distinguished from the variable ones, and thus what I believe to be the fundamental morphological characters essential to proper specific diagnoses were ascertained. At the same time due attention was also given to those characters which might be used to advantage in defining categories above or below the specific level. By using these categories as standards of differentiation, various components of the geographically distinct groups were again investigated. Taxa of the same level were placed in what I assume to be their proper status, and thus a simple scheme of classification expressing the phylogenetic relationship of different groups was constructed on the basis of morphological characters and geographic distributions. It is hoped that this scheme will not only illustrate certain principles in the evolution and distribution of the genus, but also be of some service to horticulturists and to botanists who are concerned with the identification of their *Philadelphus* material, and to cytogeneticists who are interested in the chromosome numbers and behaviors of the various forms of this genus.

In this study the determinations of the taxa are made by comparing the specimens with the types as far as they are available. Since over 40% of the binomials pertaining to this genus were based on cultivated forms with no type ever designated, and sometimes with no actual specimens preserved, material annotated by their authors or specimens prepared from plants cultivated in the gardens indicated in the original publication are used to substitute for the types. In cases like *P. inodorus* Linn. where the taxon was based entirely on a previously published plate and a pre-Linnaean description, specimens from the type locality which best matched the illustration and agreed with the description were selected for identification purposes.

My thanks are due not only to the curators of the herbaria mentioned in the foregoing paragraph for the use of the facilities in their herbaria and libraries or for generous loans of material, but also to Dr. E. D. Merrill for patiently going over a large part of the manuscript with many valuable suggestions, to Dr. C. E. Kobuski for helpful criticisms and suggestions, to Dr. I. M. Johnston for assistance in locating literature regarding North American species, to Dr. K. Sax for consultations on cytogenetic and hybridization problems, to Dr. D. Wyman for the unselfish sharing of his profound knowledge of the living plants as well as the records of the cultivated forms on the grounds of the Arnold Arboretum, to Miss E. E. Upham for her patience in answering my numerous questions concerning both English and Latin, and to Mr. H. Howard for the photographs. I am also indebted to Dr. G. Taylor, Keeper of Botany at the British Museum and Dr. Charles Baehni, Director of the Conservatoire et Jardin Botaniques, Genève. With the help of Mr. Exell, the former gave me a detailed description of the nature of the pubescence on the hypanthium, disk and style of the type of *Philadelphus coronarius* Linn. in the Linnaean Herbarium. Through Professor E. D. Merrill, the

latter sent me the photographs of Schrader's manuscript and drawings together with the photocopies of the types of Schrader's species as published in De Candolle's Prodromus.

HISTORY

The first written account of a plant belonging to *Philadelphus* is found in a Chinese poem of the eleventh century describing the fragrance, color and contrast of the white flower with the green foliage, thus: "Herbs for color, trees for shape; None in fragrance to this [Philadelphus] compare. Like white foam in a sea of green, Unique among the shrubs it has been." Although this passage, like those of Gerarde, Clusius, Bauhin and other pre-Linnaean authors pertaining to the plant, is nomenclaturally of no importance to modern taxonomists, it nevertheless indicates the antiquity of man's knowledge of the *Philadelphus*.

By the time of Linnaeus, *Philadelphus* had already become a widely cultivated plant in European gardens. In pre-Linnaean literature it appeared as *Syringa* Tournefort, *Frutex coronarius* Clusius, or *Philadelphus* Athenaci et Rivinii. Linnaeus established the genus in 1737 and validated it in 1753. He recognized two species, *P. coronarius* and *P. inodorus*, and distinguished them by their leaf margins. Accordingly, the former species is characterized by its subdentate leaves and the latter by its entire leaves. The fresh material in the gardens of Clifford and Uppsala provided Linnaeus firsthand information about *P. coronarius*. Judging from the material preserved in the Linnaean Herbarium, he correctly identified it as representing Clusius' *Frutex coronarius*. Of the second species, he saw no specimen. His binomial was based wholly on the Catesby description and plate which in turn was based on material observed at the Savannah River region on the border of South Carolina and Georgia.

From the time of Linnaeus to that of A. P. de Candolle, botanists who were interested in *Philadelphus* had their studies limited to the few species of European and American origin, especially the cultivated forms. Miller in 1768 added one dwarf species and a variety with variegated leaves. As he had a larger collection of the living plant belonging to this genus, he perhaps acquired a more intimate knowledge of the group. He had seen sterile specimens of *P. inodorus* Linn. which he raised from cuttings sent him by Dale from Carolina. As these plants were killed by frost when two years old, his records on the height of the plant, the color of the flower and the size of the fruit were probably abstracted from Catesby's accounts. Willdenow in 1809, on the basis of material cultivated in the Botanical Garden of Berlin, described *P. grandiflora*, distinguishing it from *P. inodorus* Linn. by its prominently toothed leaves. About that time, *P. inodorus* Linn. was also in cultivation in a few gardens in England. Sims in 1812 on the basis of a specimen sent him by Whiltey of the Fulham Nursery prepared a colored plate and a description for that species.

During this period, with the exception of Nuttall and Michaux, authors

on American flora had a very dim concept of the published species of American *Philadelphus*. Walter (1788) in the Flora Caroliniana presented a very general account of *P. inodorus* Linn. After comparing his statements about this species with that of Linnaeus, one has a feeling that he had never seen a specimen of it for he used even the same wording as Linnaeus. Michaux, being a true field naturalist, had seen the plant and in his Flora Boreali-Americana published in 1803 he used hitherto unknown characters about the long acuminate sepals, suboval petals and elongated undivided style for distinguishing *P. inodorus* Linn. Pursh in 1814 recognized four species, one of which, *P. lewisii*, was new. According to the material he cited, he probably had not seen any *P. inodorus* Linn. in America. His description was based on Sims' illustration and the cultivated material in England. Elliott in 1821 admitted that he had seen no specimen of *P. inodorus* Linn. in the various collections of dried plants which he had examined. He further stated that the plant was so rare in nature that no botanists in his day had seen it in the woods.

Nuttall in 1817 described *P. hirsutus* on the basis of his own collection from the bank of the French River near Warm Springs, Tennessee. His description of the species indicates that he was a man of keen and accurate observations and consequently his treatment gives the truest picture of the genus up to his time. He recognized four species. As three of them were American in origin, he was led to conclude that *Philadelphus* is "a North American genus, with the exception of *P. coronarius*." With our present knowledge of the genus, there is a great deal of truth in this statement, for not only the largest numbers of species of the genus occur in North America, but the principal morphological changes of the group are also found here.

Schrader was the first man who attempted to study the entire genus extensively. His dissertation on *Philadelphus* with illustrations which has been cited by De Candolle and Loudon has never been published. The manuscript is preserved in the Conservatoire et Jardin Botaniques, Genève. Part of it was incorporated by De Candolle (1828) in his Prodromus III. After Schrader's death, in the "Reliquiae Schraderianae" published in Linnaea (1838), an improved form of that dissertation appeared again, but without illustration. In the manuscript as well as the latter paper he included nine species and four varieties of *Philadelphus*. Unfortunately his material was largely limited to the forms then cultivated in European gardens. Having no access to specimens representing species already described by American botanists, he created several synonyms. Moreover, he accepted garden sports or hybrids as representing species and thus created additional confusion. He divided the then known species into two sections on the basis of the habit and the inflorescences, but assigned no sectional names to them. In the section "Caulibus crassioribus strictis. floribus racemosis" he recorded five species and three varieties. The rest were placed in the section "Caulibus tenuioribus virgatis laxis, floribus solitariis ternisve." Schrader's conclusions, whether correct or incorrect,

were followed by European botanists and horticulturists for over half a century.

De Candolle in 1828, using Schrader's manuscript as a standard, published a comprehensive treaty on the genus. He recognized eleven species and three varieties. For the three extra American species not included in Schrader's manuscript, he simply annexed them to Schrader's order and placed them all in the slender-stemmed and solitary-flowered group. This represents a very indiscriminate treatment, for closely related species like *P. coronarius* Linn. and *P. lewisii* Pursh, which are alike in their habit and inflorescences, were placed in separate sections.

Loudon in 1833 in Arboretum et Fructicetum Britannicum gave an illustrated comprehensive account of the genus. He recognized ten species and four varieties, placing them in two sections. In the "Stems stiff and straight. Flowers in Racemes" section he included six species and four varieties and in the "Stems more slender, rambling, twiggy and loose. Flowers solitary, or 2 or 3 together" section he had four species. In this classification what we now interpret as inseparable entities, like *P. inodorus* Linn. and *P. grandiflorus* Willd., were placed in different sections.

Philadelphus from Asia and Central America did not appear in botanical literature until the eighteen thirties. Wallich was the first person to discover a species of *Philadelphus* from Asia. In 1831 he named the specimens procured from Gossainthan, Sirmore and Kamaon as *P. tomentosus* and *P. triflorus*. G. Don in 1832 validated the first binomial by giving it a description and Royle in 1839 prepared a colored plate for this Himalayan taxon.

Schlechtendal in 1839 on the basis of Schiede's collection from Jalapa and Ehrenberg's collection from Carmen described *P. mexicanus*, the first species of *Philadelphus* from Central America. About the same time, Bertoloni (1840) published an illustrated account of a Guatemala species under the name *P. myrtoides*, a species which marks the southmost limit of the spontaneous distribution of the genus.

A. Gray in 1849 on the basis of Fendler's collection from Santa Fe Creek, New Mexico, published *P. microphyllus*, the first known xerophytic species. The plant was introduced to Europe in 1883 and hybridists there took advantage of its low habit and very agreeable fragrance and in the autumn of 1887, the Lemoine Nursery of Nancy, France, put into commerce a novelty under the name, *P. lemoinei*, which was announced to be the result of a cross between the American small-leaved species, *P. microphyllus* Gray and the much cultivated European species, *P. coronarius*.

Lindley and Paxton in 1852 published *P. satsumi* Sieb., the first known species of *Philadelphus* from Eastern Asia, on the basis of both living material introduced and the herbarium specimens prepared by Siebold from Japan. Ruprecht in 1856, in a paper of Maximowicz on the important trees and shrubs of the Amur Region, described *P. tenuifolius*, the first known species of *Philadelphus* from the Eastern Asia mainland. A year later in a discussion about *P. tenuifolius* he accidentally published *P. pekinensis* which became the first known Chinese species in the genus.

By the middle of the nineteenth century *Philadelphus* introduced from America and Asia were cultivated under thirty odd names in European gardens. Botanists and growers began to be conscious of the confusion and tried to clarify the nomenclature and to identify the plants. The general tendency shows a lumping effort. Koch in 1859 in an article titled, "Notes on the Genus *Philadelphus*," first published in Germany and then translated by De Borre into French, recognized 16 species. Ten years later, in his Dendrologie he reduced the number to 11 species. His species concept was rather vague and he clearly erred in making species of American and Asiatic origin conspecific entities. His work created confusion rather than clarification. Maximowicz in 1867, in a "Revisio Hydrangearum Asiae Orientalis," treated all the species of *Philadelphus* that had racemose inflorescences, including those from Europe, Caucasus, Himalayan Regions, eastern Siberia, northeastern China, Japan and North America, as varieties of *P. coronarius* and thus created a large number of synonyms.

Koehne was the best authority of the group, and he was careful and keen in his observations. Unfortunately the diagnostic characters he chose to delimit subsidiary groups between the species and the genus do not at all well cover the characters of the species involved, and his arrangement proved to be impracticable. In 1893 he selected the exfoliation of the bark as the most important character for distinguishing major groups. He divided the genus into the Corticatae, including those species with closed bark and the Decorticatae containing those with exfoliate bark. Realizing this character to be unreliable and the scheme not workable, three years later, he selected the size of the stigma as the distinguishing character for dividing major groups. On this basis he proposed two sections, the Poecilostigma and the Stenostigma. His section Poecilostigma represents a conglomeration of phylogenetically unrelated species. This section was subdivided into three subsections, the Gemmati with exposed buds, the Microphylli containing species with inclosed buds, small leaves and united and more or less separated stigmas; and the Speciosi including species with inclosed buds, large leaves and separated broad stigmas. His section Stenostigma represents species with inclosed buds and separated narrow stigmas. This was subdivided into four subsections; the Paniculati with paniculate inflorescences, the Gordoniani with racemose inflorescences, decorticate branchlets and late flowering individuals, the Satsumani with racemose inflorescences, decorticate branchlets and early blooming individuals, and the Coronarii with racemose inflorescences, corticate branchlets and usually early flowering individuals. In this classification Koehne failed to give a single character which holds true for the Poecilostigma as a section, and for the demarcation of the Stenostigma he gave two characters, that is, the narrow stigmas and the inclosed buds. At first his statement seems to be acceptable. But as one examines the species that Koehne placed in the Stenostigma section, one finds that this section cannot stand as a taxonomic unit, for the first listed species *P. californicus* Benth. has exposed axillary buds, a character which is not

supposed to exist in the section. Moreover, the differences in the size and shape of the stigmas between species of this section is just as great as are those in Poecilostigma. As to the characters he chose for distinguishing subsections they are not strong enough even for delimiting species. The manner of the peeling of the bark and the time of blooming are subjected so much to the environmental changes that they are not of much value except for distinguishing closely related garden forms planted in similar conditions. Although Koehne's system of classification has been followed by many authors including Engler in his treatment of the genus in the second edition of Die Natürliche Pflanzenfamilien, it is not adopted in this study, for it represents a more artificial and less phylogenetic system.

The beginning of the twentieth century seems to mark a new tendency in the study of *Philadelphus*. Botanists began to show interest in the group on a regional basis. Beadle in 1902 concentrated in a study of *Philadelphus* of the southeastern United States and proposed three new species and one new variety from the homeland of *P. inodorus*. His findings were the basis for the treatment of the genus in Small's Flora of the Southeastern United States (1903, 1913) and the Manual of the Southeastern Flora (1933) of the same author. He introduced the shape of the base of the capsules for distinguishing species. Thus he characterized *P. inodorus* as a species in which the base of the fruit attenuates into the pedicel and distinguished his new species, *P. gloriosus* from *P. inodorus* by the abruptly contracted fruit base. This character has never been used by any other botanist in the classification of *Philadelphus*. As the shape of the base of the capsule in this genus depends upon the fullness of the fruit which in turn depends partially upon the environmental conditions and partially upon the time when the specimens are collected, it has little value for specific identification.

Rydberg in 1905 prepared a comprehensive treatment of the genus for North America. The principal diagnostic characters he used were the presence or the absence of hairs on the style and disk which he called the upper free part of the ovary, the number of flowers on a flowering branch and the size of the leaf. He recognized 36 species, 10 of which were new. In the key, he grouped those species into six subdivisions, the Californici, Coronarii, Grandiflori, Hirsuti, Microphylli and Mexicani. His work indicates his ability in recognizing differences, and most of his species are good ones. Although some modern botanists may prefer to place the taxa he recognized in subspecific rank, that is only a matter of opinion which does not affect those taxa being distinct entities.

Nakai in 1915 considered the species of Japan and Korea, recognizing seven species, two of which were new. On the basis of bark characters of the second year's growth, whether closed or exfoliate, he raised two of Koehne's subsections into sections. In Satsumani he placed a single species, *P. satsumi* and in *Coronarii* he placed all the other species.

Rehder (1920, 1927, 1940, 1949) considered chiefly the cultivated species and varieties. In 1927 he subdivided the genus into six groups:

1. Gordoniani, 2. Sericanthi, 3. Coronarii, 4. Speciosi, 5. Microphylli and 6. Gemmati. Later (1940) he definitely designated these groups as Series. The characters he employed in the key were the number of flowers on a flowering branchlet, the pubescence on the hypanthium, the color of the calyx, etc. He was at times inconsistent when, as an example, he separated a group of species by the pubescence on their hypanthia, yet under certain species of this category he recognized varieties with glabrous hypanthia. as in the case of *P. pubescens* Loisel. var. *intectus* (Beadle) Moore. The diagnostic characters for a series do not always agree with his key characters, as in the case tof *P. purpureo-maculatus* Rehd. In the text, he placed this species in series Microphylli which is characteristically a taxon with hidden buds while in the key it is placed under the category of exserted buds. His series concept impresses me as rather vague for in some cases a series consists of species different from each other in many respects. Thus in Series Gordoniani, he placed *P. californicus* Benth. with paniculate inflorescence, glabrous hypanthium and exposed buds as well as *P. pubescens* Loisel. with racemose inflorescence, pubescent hypanthium and inclosed buds; and in Series Sericanthi he placed *P. sericanthus* Koehne with pubescent hypanthium and also *P. delavayi* L. Henry with glabrous hypanthium. Moreover, in some cases morphologically inseparable and geographically closely affiliated taxa like *P. tomentosus* Wall and *P. delavayi* L. Henry are allotted to different series. Rehder's identification formed the basis for Bangham's chromosome count of the genus, and his taxonomic units were adopted by Janaki Ammal in her discussion on the classification and geographical distribution of *Philadelphus*. Rehder's material was restricted to the cultivated species of the temperate regions. This geographical limitation combined with the short-comings of his classification consequently affected the value of the conclusions drawn by the cytologists.

Hitchcock in 1943 studied the American xerophytic species. His work contributes materially to an understanding of the group. He considered four species and thirteen subspecies, all placed in what he called the Microphylli group. According to him, these small-leaved species, "As a unit . . . are readily distinguished from all other North American species of *Philadelphus*, yet it is quite apparent that they have been derived from, and are very closely related to, certain species of the *Mexicani*." I have carefully examined all the taxa that Hitchcock considered as representing a single group, and I can only conclude that this "group" includes heterogeneous elements. The small leaved character impresses me as being misleading. The comparative study of the morphological characters and geographical distribution of all the species of the genus indicates that the elements native of the region considered by Hitchcock are end products of evolution stemming from two or three directions. It is true that three of the four species in Hitchcock's treatment, *P. serpyllifolius* Gray, *P. purpusii* Brandeg. and *P. mearnsii* Evans are related to the Mexican elements. But *P. microphyllus* Gray and its related taxa are surely distant from them in their phylogenetic relationships. In my

judgement his conclusion on *P. microphyllus* Gray being a derivative of *P. purpusii* Brandeg. is too arbitrary. Before me there are several specimens from the Northern Rocky Mountains, chiefly Montana, with characters intermediate between *P. lewisii* Pursh and *P. microphyllus* Gray. The size, form and texture of the leaves and the size of the flowers of these specimens are typical of *P. microphyllus* Gray, but some, or rather, most flowering branchlets possess five flowers which is characteristic of *P. lewisii* Pursh. These spontaneous intermediate forms are good evidence of the origin of *P. microphyllus* Gray and its related species. Nevertheless, Hitchcock's paper takes high rank among all those published on the genus. I believe that it was unfortunate that his studies were limited to the small-leaved forms, for leaf size is indeed an unreliable character, and generalizations can scarcely be made except on the basis of a critical study of all species of the genus.

From the late 1920s up to the present the discoveries of botanists in fields other than taxonomy have broadened our knowledge of *Philadelphus*. Bangham in 1929 [1] published the result of his observation on the chromosome number of the genus. Janaki Ammal in 1951 [2] treated the subject in greater detail and discovered triploid and aneuploid individuals in garden forms. These findings will eventually help breeders to obtain better garden forms, for by suitable mating of parents of known chromosome compositions, better hybrids with triploid, or perhaps tetraploid or aneuploid chromosome makeups can be induced. As in many ornamental plants some extra chromosomes often enhance their horticultural merits.

Chaney in 1939 and Condit in 1944 [3] confirmed the occurrence of fossil *Philadelphus* in the middle upper Miocene. The fossil *P. nevadensis* (Knowlton) Chaney resembles the leaves of *P. lewisii* Pursh which now occurs in northwestern United States. This discovery advances our understanding of the present distribution of the species in this genus.

EVALUATION OF MORPHOLOGICAL CHARACTERS IN THE CLASSIFICATION OF THE GENUS

In the historical review of *Philadelphus* studies I have noted that the habit of the plant, the color and exfoliation of the branchlets, the position of the buds, the size, texture, dentation and indumentum of the leaves, the inflorescences, and the floral parts have all been used either as major or minor diagnostic characters in the classification of the species of the genus. Individual authors have stressed different points and consequently their systems of classification lack uniformity. In the following discussion an attempt is made to evaluate characters stressed by others as well as to add certain fruit and seed data.

[1] The Chromosomes of Some Species of the Genus Philadelphus. Jour. Arnold Arb. **10**: 167–169. 1929.

[2] Chromosomes and the evolution of Garden Philadelphus. Jour. Royal Hort. Soc. **76**: 269–275. 1951.

[3] R. W. CHANEY, Pliocene Floras of California and Oregon, Carnegie Inst. Washington Publication 553. p. 79. pl. 16. fig. 2. 1944.

Habit: The habit was used as a principal criterion for separating major groups by early authors like De Candolle and Schrader. As our knowledge of the genus increased, the importance of the habit in the classification of *Philadelphus* gradually decreased. Judging from plants cultivated in the Arnold Arboretum, there seems to be no correlation between the habit of the plant and the other morphological characters such as the position of the buds, or the number of the flowers. Moreover, the habit is often affected by the environmental conditions and the age and vitality of the plant. Possibly the habit, such as upright tall stiff shrub, low widely spreading shrub with twisted branchlets, low compact shrub with upright branches or moundlike tall shrub with arching branchlets, may be used for recognizing special horticultural forms, varieties or even species, but it should not be used for distinguishing taxa above these ranks.

Branchlets: In general practice, a few branchlets constitute the only material a herbarium taxonomist may have for purposes of study and identification. Regarding the branchlets of *Philadelphus*, my discussion will be carried on under the headings of the second year's growth, current year's growth, the axillary buds, and the adventitious growth.

The color and exfoliation of the bark of the second year's growth, whether closed or exfoliate, has been employed by Koehne, Rehder and others for distinguishing species or even taxa of higher rank. It is true that the bark of certain species such as *P. pubescens* Loisel. and its related forms are prevailingly gray. But that of the other species is of various shades of brown, from ash-brown to reddish chestnut. In some species the bark exfoliates in sheets. In others they slowly wear off. It seems to be apparent that the size and the age of the shoot, the rainfall of the growing season, and the amount of snow in the preceding winter are all contributing factors effecting the exfoliation of the bark. Often different shoots on the same plant differ in the degree of exfoliation. As the herbarium specimens represent only very small portions of an individual plant, the actual selection of specimens may govern the evident exfoliation and bark color very materially. When only a few specimens are available, one may interpret the bark color and exfoliation of the second year's growth as forming a definite criterion for species delimitation, but when many specimens from the same general area are examined, the intergradations in color and exfoliation should convince any one that these characters are of little value in recognizing species.

The current year's growth of all species of *Philadelphus* are of two kinds, the sterile shoots bear leaves only, and the flowering shoots each of which bears one to three (or very rarely more) pairs of leaves and a terminal flower or a cluster of flowers. The sterile shoots are more vigorous and their leaves are larger and comparatively more dentate than are those of the flowering branchlets. The bud position on these shoots is very constant.

In one group, the buds are hidden in nodal pouches at the ends of the petioles (Pl. I, fig. 3). When the leaves fall, these buds are covered by

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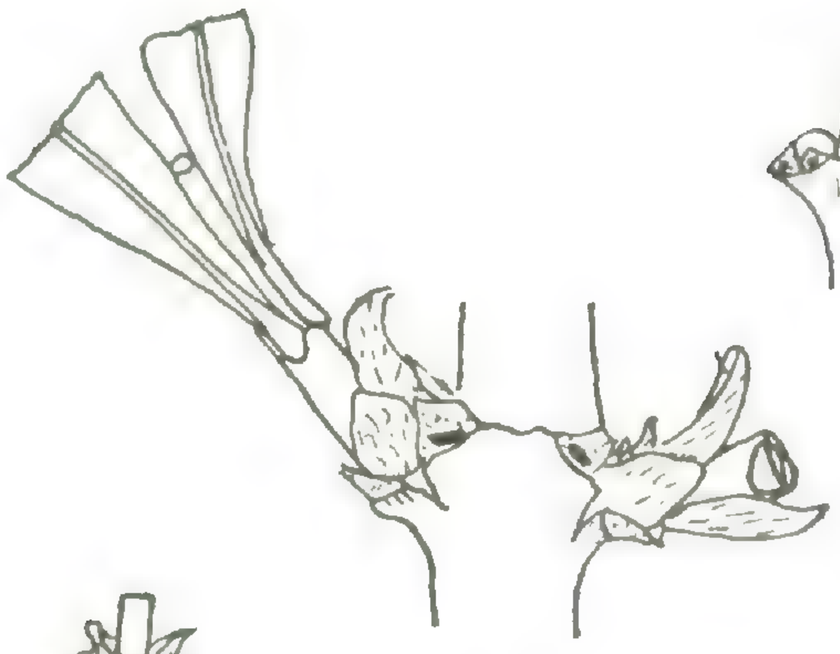
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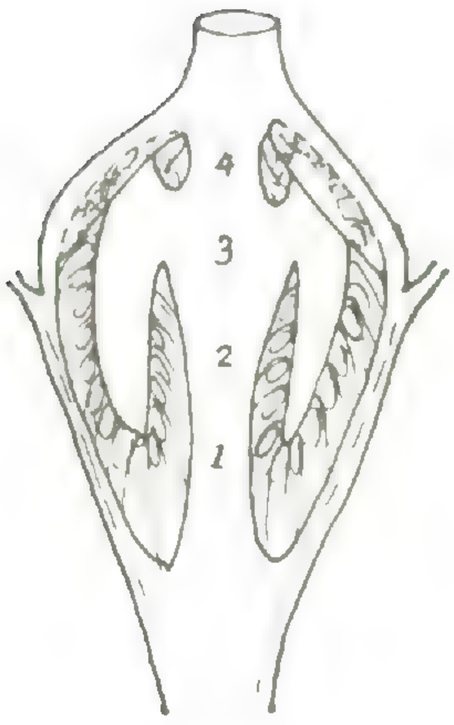
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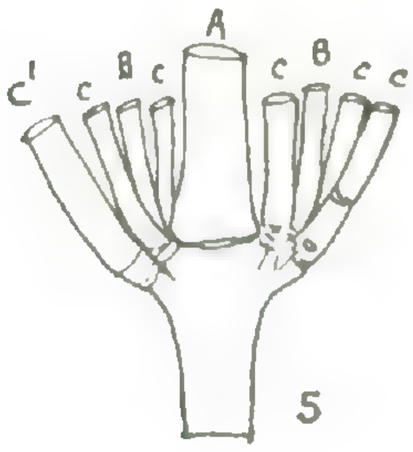
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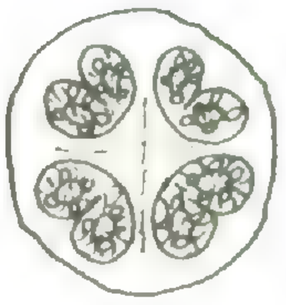
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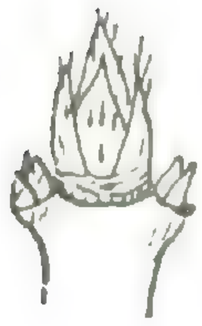
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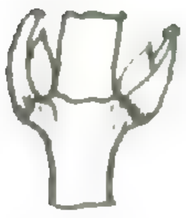
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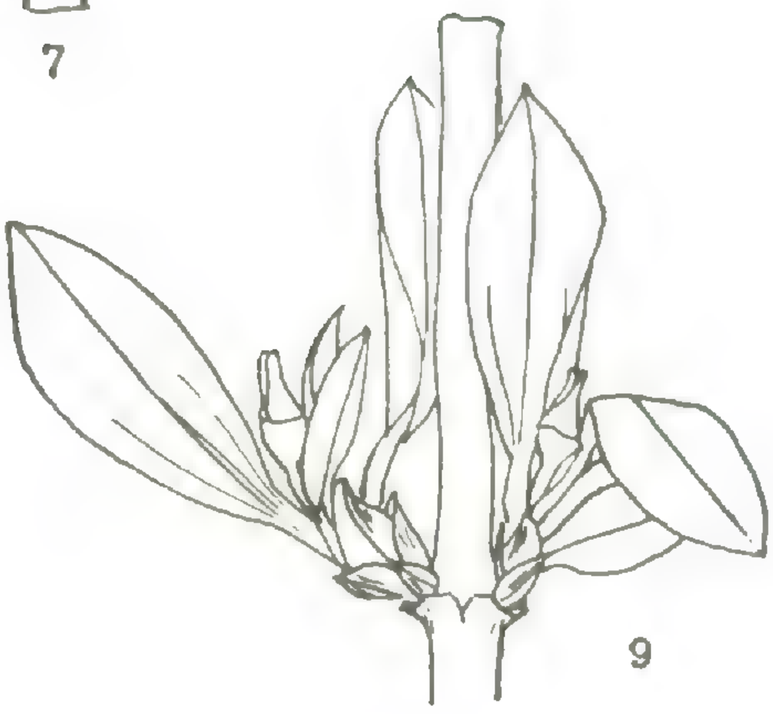
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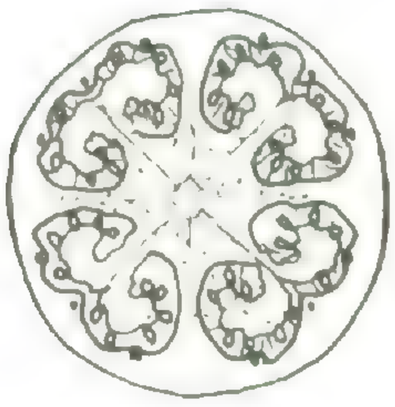
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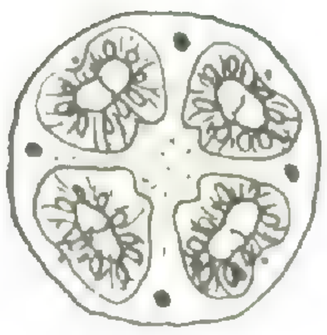
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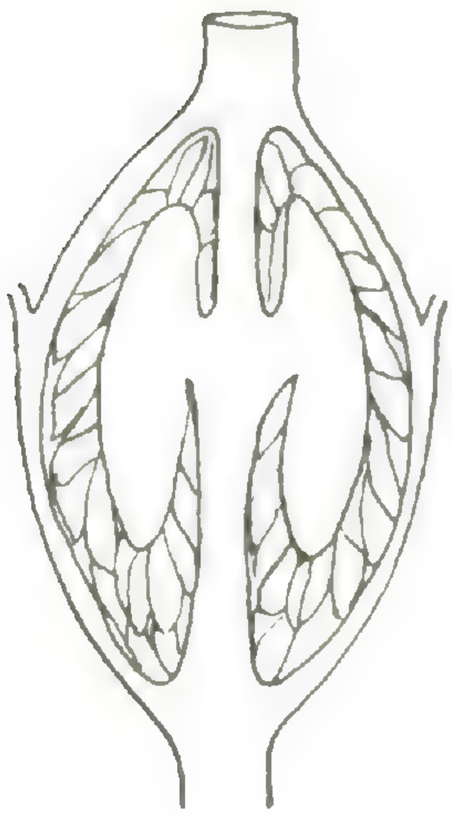
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the abscission layers (Pl. I, fig. 1a, 1b, & 2). As these buds unfold, they burst open the abscission layers (Pl. I, fig. 4) which persist for a long time at the base of the new branchlets. All the plants with such hidden axillary buds bear no terminal buds. Their shoots are determinate. All the Old World species of *Philadelphus* and many of those of the New World are characterized by such hidden buds and determinate branchlets.

In contrast, other species bear prominent conical axillary buds on their sterile and flowering shoots at anthesis (Pl. I, fig. 7, 8). In general, nodes bearing these buds are strongly curved below the insertion of the leaves, while those with hidden buds are but slightly curved. It is doubtful if latitude and temperature have any effect on the production and size of the exposed buds. Thus, *P. hirsutus* Nutt. is a native of the southern Appalachian Mountains, but when cultivated in Boston, which is nearly seven degrees higher in latitude than the original home of the species and Boston has an average annual minimum temperature 10–15 degrees lower than Nashville where the plant grows wild, its axillary buds at anthesis are just as prominent as are those on the Tennessee specimens. Moreover,

PLATE I

1. Shoot apex of the determinate type (× 4, from fresh material collected in the Arnold Arboretum, Jan. 20, 1952). 1a. *P. coronarius* with the lateral buds completely covered by the abscission layer. 1b. *P. microphyllus* with the lateral buds more or less unfolding, the dead terminal portion of the branchlet is more prominent here. 2. Node of *P. delavayi* after the leaves have fallen, showing the lateral buds covered by the abscission layer (× 4, *Rock 16637*). 3. Node of *P. maculatus* with the ends of the petioles attached, showing prominent nodal pouches containing the buds; the curves below the insertion of the leaves are gentle (× 4, *Mueller 2213*). 4. Node of *P. delavayi* with the axillary buds unfolding and each abscission layer has burst open (× 3, *Rock 16173*). 5. Node of a sucker; A, with two branches B, developed from normal axillary buds and six branches developed from adventitious buds. Five of the six are flowering shoots C, and one is a vegetative shoot C′. 6. Shoot apex of the indeterminate type, *P. hirsutus*, with a large terminal bud and two small lateral ones (× 4, from fresh material collected in the Arnold Arboretum on Jan. 20, 1952). 7. Node of *P. texensis* with the petioles on, showing the exposed axillary buds, the curves below the insertion of the leaves are sharp. (× 4, *Reverchon 1523*). 8. Node of *P. hirsutus* after the leaves have fallen, showing two lateral buds exposed (× 4, fresh material collected in the Arnold Arboretum, Jan. 20, 1952). 9. Node of *P. mearnsii* after the buds are unfolded. The unfolding of the buds does not affect the leaf-scars (× 5, *Palmer 11492*). 10. Longitudinal section of a fruit of *P. inodorus*, 1 week after anthesis, showing the attachment of the placentas which are above the insertions of the sepals (× 10). 10a, 10b, 10c, and 10d are transverse sections of the above cut through the points 1, 2, 3, and 4. 10d appears 8-locular. 11. Longitudinal section of a fruit of *P. microphyllus*, 2 months after anthesis, showing the attachment of the placentas which are about the same level as the insertions of the sepals (× 10). 12. Longitudinal section of a mature fruit of *P. hirsutus* showing the attachment of the placentas which are below the insertions of the sepals (× 10).

such plants often bear strong terminal vegetative buds (Pl. I, fig. 6), therefore their shoots are indeterminate. All the species with exposed buds occur in the New World.

The presence or absence of exposed buds is not only constant, but the buds are also very easy to detect. As long as the leaves are mature, no matter whether the branchlets be sterile or fertile, the buds are evident. The morphological constancy and the geographical coincidence indicate that the position of the buds whether hidden or exposed, is a very good character for separating major groups in *Philadelphus*. Accordingly, in this study I take this character as one of the key categories for delimiting the subgenera of the genus.

All species of *Philadelphus* produce adventitious buds at the basal portions of their principal stems or along the upper parts of their branches. In the first case, the buds develop into strong sterile shoots which give rise to flowering branchlets in the following year. In the second case, the buds may develop into a weaker sterile shoot (Pl. I, fig. 5, c′), or usually they form weak flowering branchlets, (Pl. I, fig. 5, c). The leaves of such shoots are generally smaller and the flowers fewer than are those developed from normal buds. The presence of a number of such small flowering branchlets gives the stem somewhat the appearance of a brush. A branch with multiple branchlets at its nodes should always be taken as a sign of old age and reduced vitality in the plant.

Leaves: Authors of the first few species of *Philadelphus* relied chiefly on leaf characters for distinguishing them. Thus Linnaeus distinguished *P. inodorus* from *P. coronarius* by its entire leaves and Willdenow distinguished his *P. grandiflorus* by its dentate leaves. When only a few specimens are compared, there may be seemingly marked differences in the size, shape, texture, venation and margin of the leaves. But when a large number of specimens are available for comparative study, the gradual changes exhibited in these respects prove that what various authors such as Schrader, Koch, Maximowicz, and Rydberg accepted as differential specific characters are not constant. In fact, there is little difference in the size and shape of the leaves of the species of *Philadelphus* of any single area, and also often even between species from distant regions with similar climatic conditions. The differences that existed in the size, shape, texture and margin of related species may also occur as modifications among representative specimens from the same species differing only in age and vigor. Therefore the size and shape in the leaves can only be used as supplementary criteria for distinguishing varieties or garden forms and occasionally even species when it is correlated with characters furnished by flowers and fruits.

The leaves on the sterile shoots and those on the flowering shoots of an individual plant differ in size, shape, apex and margin. In general the leaves on the sterile shoots are larger, more acuminate at the apex, more coarsely dentate at the margin, more pubescent on the surface and even broader at the base than are those on the flowering shoots. Yet, leaves of a flowering shoot developed from an adventitious bud are always much

smaller, more acute, more subentire and more glabrous than are those developed from normal buds. One judges that the age of the plant, the vigor of the shoot, the available water supply may be reflected in the leaves of *Philadelphus*. For this reason, leaf characters based on these aspects should not be employed for the delimitation of taxa above varieties or garden forms.

The nature and the density of the indumentum on the leaf surfaces are rather constant as to leaves on comparable shoots of a species. They usually correlate with certain flower characters, therefore may be used as auxiliary criteria for distinguishing species or categories of even higher rank, such as section and series.

Inflorescences: *Philadelphus* as a genus is characterized by determinate terminal inflorescences, each with 1 or 3 flowers at the last node, and none, one, rarely two single flowers, or very rarely a cyme in the axil of a bract or a leaf on each side of the succeeding nodes. When the succeeding node bears no flower, the branchlet has solitary or ternate flowers. When the succeeding nodes bear flowers the plant has racemose or paniculate inflorescences, depending on the number of flowers in the leaf axils. In many species the bracts are small and caducous. Since De Candolle in 1828 used the term raceme to describe *P. coronarius* Linn. and its related species, it has been used in reference to those species with a terminal cluster of flowers in all major treatments of the genus. But actually when the order of blooming is taken into consideration, none of the *Philadelphus* species really bear true racemes. In this genus, the first opened flower always prohibits the elongation of the flowering shoot and limits the formation of more flower buds. The figures on Plate II actually represent the number of flowers and their relative developments on the branches of *P. californicus* Benth., *P. pubescens* Loisel., *P. lewisii* Pursh, *P. pekinensis* Rupr., *P. inodorus* Linn., *P. microphyllus* Gray, *P. falconii* Sarg., *P. karwinskyanus* Koehne, *P. myrtoides* Bertol., *P. mexicanus* Schlecht., *P. hirsutus* Nutt. and *P. serpyllifolius* Gray. In each case the flowers at each node behave as an independent unit. In cases where many flowers are formed at the end of the flowering branch the terminal one always opens first. Such inflorescence is a determinate raceme or a panicle.

Philadelphus inflorescences may be roughly arranged in six general types, the paniculate, the determinate-racemose, the pauciflorous, the ramiferous, the mexicanus, and hirsutus types. The paniculate type includes inflorescences composed of simple or more or less compound cymes (Pl. II, fig. 1). It is represented by *P. californicus* Benth. and *P. cordifolius* Lange. The determinate-racemose type is the commonest type of inflorescence in the genus. It is best represented by *P. pubescens* Loisel. and *P. lewisii* Pursh in the United States, *P. satsumi* Sieb. of Japan, *P. tenuifolius* Rupr. of the Amur Region, *P. pekinensis* Rupr. and all the other Chinese species, *P. tomentosus* Wall. of the Himalayan Region and *P. caucasus* Koehne and *P. coronarius* Linn. of Caucasia and southwestern Europe. It consists of 3, or very rarely 1, or occasionally in *P. coronarius* Linn. 5, terminal flowers and several pairs of axillary ones at the suc-

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ceeding nodes (Pl. II, fig. 2–5). Sometimes, as in *P. coronarius* Linn., a pair of flowers may appear in a single leaf axil. The upper axillary flowers are often subtended by bracts which fall early in the flowering season. The lower axillary flowers are in general subtended by normal leaves. Great variations exist in the number of flowers in a cluster, the length of the central axis and the size of the bracts in specimens representing a species or sometimes even from a single plant. This is especially true in *P. lewisii* Pursh and *P. pekinensis* Rupr. It seems that the age and vitality of the shoots which give rise to the flowering branches are the controlling factors for such modifications. There are certain garden forms characterized by a predominantly short flowering axis. In such cases the clusters appear rather compact (Pl. II, fig. 4, 5). There are certain species which bear loose determinate-racemes. In such cases the lower two pairs of flowers are borne in the axils of normal leaves (Pl. II, fig. 2, 3); the inflorescences of *P. pubescens* Loisel. and *P. intectus* Beadle are typically of such form.

The pauciflorous type consists of inflorescences with one or three terminal flowers on shoots devoid of exposed axillary buds. This type is best illustrated by *P. inodorus* Linn. and *P. microphyllus* Gray (Pl. II, fig. 6, 7) and their related species. In certain garden forms, the lateral flowers of this type may be replaced by two cymes with elongated peduncles. In such cases, a true dichasium is formed (Pl. II, fig. 8).

The ramiferous types of inflorescences are depauperated panicles. They may appear as racemes or panicles, but each individual flower is on a short pedicel jointed to a woody axis. Thus each flower stalk is morphologically composed of a peduncle and a pedicel. In *P. myrtoides* Bertol. the peduncles of the lower flowers are as long as those of the upper one and the inflorescence appears more or less racemose, but the individual pedicels are jointed (Pl. II, fig. 10). In the more ramified form, as represented by *P. karwinskyanus* Koehne, the inflorescence is composed of elongated lower branches (Pl. II, fig. 9) and shorter upper ones, and it appears like a panicle. Some of the lower branches even bear axillary buds on their basal nodes.

The mexicanus type has one or three terminal flowers on short but jointed stalks, as found in *P. mexicanus* Schlecht. Such an inflorescence

PLATE II

TYPES OF INFLORESCENCE IN PHILADELPHUS (all × ½). 1. The PANICULATE TYPE, *P. californicus* (*Abrams 4649*). 2–5. The DETERMINATE-RACEMOSE TYPES. 2. *P. pubescens* (*AA 2221*). 3. *P. lewisii* with 3 terminal flowers (*Thompson 10522*). 4. *P. lewisii* with 1 terminal flower (*Engberg*, June 19, 1905). 5. *P. pekinensis* (*Hers 2515*). 6 & 7. The PAUCIFLOROUS TYPE. 6. *P. inodorus* (*AA 4159–1*). 7. *P. microphyllus* (*Fendler 266*). 8 TRUE DICHASIUM, *P. falconeri* (*Hu*, June 14, 1951). 9 & 10. The RAMIFEROUS TYPE. 9. *P. karwinskyanus* (*FGW 872*). 10. *P. myrtoides* (*Carlson 435*). 11. The MEXICANUS TYPE, *P. mexicanus* (*Standley 65124*). 12. The HIRSUTUS TYPE, *P. hirsutus* (*Palmer 35517*). 13. The SERPYLLIFOLIUS TYPE, *P. serpyllifolius* (*Cary 9435*).

is probably a reduced or simplified compound inflorescence with the portion above the bracts representing the pedicel and the portion below the joint, the peduncle.

The hirsutus type, as represented by *P. hirsutus* Nutt. and *P. mearnsii* Evans, has inflorescences of solitary or ternate flowers on short flowering branches with exposed axillary buds (Pl. II, fig. 12, 13). Such inflorescence often develops from a terminal bud.

The type of inflorescence in *Philadelphus* is a definite and easily recognizable character. When correlated with the position of the buds, the form of stigma, the shape of fruit, and the appendages of the seed, the type of inflorescence can be employed as a very useful device for distinguishing sections of the genus as well as for assisting in placing the species in its phylogenetic position. In using the inflorescence in the classification of *Philadelphus* several essential points should be observed. (1) All the inflorescences of *Philadelphus*, no matter whether they are composed of a single flower, or three or five up to 20 flowers in simple or ramified branches, are borne at the end of current year's growth. In other words, they are all derivatives of individual buds which are usually axillary. (2) All of them are determinate inflorescences; that is, the terminal flower in each type opens first and they thus limit the elongation of the floral axis. (3) The type of inflorescence of a species is definite, but the number of flowers on each flowering branch is variable. A species with pauciflorous type of inflorescence may have some branches with a single flower, some with three and others with a true dichasium of seven or nine flowers. This variation seems to be a reflection of the environmental condition of the plant as well as the physiological state of the particular flowering branch. In the cultivated *Philadelphus*, good soil, sufficient water supply, proper pruning, vigor of the plant and the bearing year always induce a large number of flowers on a branch. In case of the determinate-racemose type of inflorescence the floral axis is always lengthened.

Rickett in 1944 discussed the inflorescences of *Philadelphus* at length. He used *P. coronarius* Linn., *P. californicus* Benth., *P. lewisii* Pursh, *P. argenteus* Rydb. and *P. hirsutus* Nutt. to illustrate a hypothesis that the terminal dichasium is ancestral in *Philadelphus*. He maintained that this primitive type can be found in *P. hirsutus* Nutt., and suggested that the present forms of the inflorescences of *Philadelphus* are evolved through the reduction of the terminal dichasium to a single flower as found in *P. argenteus* Rydb. Further reduction of the lateral flowering branches leads to the production of axillary flowers of *P. coronarius* Linn. This condensation is accompanied by a lack of dormancy in the new axillary buds, which open the same season as the leaves which subtend them. From flowering branches formed in such a way, derived the floral arrangement as seen in *P. lewisii* Pursh and also the thyrse of *P. californicus* Benth., the latter represents a condensation of the second order, that is, not only are a number of the original flowering branches laterally disposed on a central rachis, but several groups thus constituted are similarly disposed on the main axis of the thyrse. According to this hypothesis the

evolution of the inflorescences of *Philadelphus* has been brought about merely by reduction and condensation of the flowering branches. As I understand the morphology of *Philadelphus*, certain assumptions accepted by Rickett apparently do not conform to what are found in nature. First he selected the inflorescence of *P. hirsutus* Nutt. to represent the ancestral form, but this species is morphologically highly specialized and its low point of placentation and its ecaudate seeds all indicate its advanced position in the evolution of the genus. Secondly, he maintained that the inflorescence of *P. argenteus* Rydb. is a derivative of that of *P. hirsutus* Nutt., but these two species are phylogenetically very remote. They belong to different subgenera. Thirdly, the condensation processes that he assumed to take place between *P. argenteus* Rydb. and *P. coronarius* Linn. and between *P. lewisii* Pursh and *P. californicus* Benth. involve more than a single year's growth. The plant part he took from *P. argenteus* Rydb., or *P. lewisii* Pursh to illustrate his principle represents two year's growth with twigs bearing buds on part of old wood and what he took from *P. coronarius* Linn. or *P. californicus* Benth. represent a single year's growth, originated from a single winter bud. When he assumed that the branch of *P. lewisii* Pursh with a number of flowering branches laterally disposed to be condensed on a central rachis to form an inflorescence corresponding to those of *P. californicus* Benth., he overlooked the age differences of the two elements involved. It is not possible within the organization of the plant to attain such assumed condensation. Moreover a shoot of *P. lewisii* Pursh that bears laterally disposed flowering branches never possesses a terminal bud, so that it is impossible for that shoot to be condensed on the main axis of the thyrse to form a paniculate inflorescence of *P. californicus* Benth. which ends with a terminal flower. Moreover, *P. coronarius* Linn. and *P. lewisii* Pursh have the same determinate-racemose type of inflorescence. When one takes into consideration all factors, it is unnecessary to invoke imagination to explain the evolution of the inflorescences of *Philadelphus*. Rickett was perhaps right in assuming the terminal dichasium as the ancestral type. He was partly correct in recognizing reduction and condensation as a process that brings about the various forms of inflorescences in *Philadelphus* but unfortunately he chose the inflorescence of *P. hirsutus* Nutt. to represent the primitive model. The most primitive type of inflorescence in *Philadelphus* is the pauciflorous type as found in the true terminal dichasium of a healthy vigorously growing flowering branch of *P. inodorus* Linn. Normally such dichasia may be reduced to three or a single terminal flower. The solitary or ternate terminal flower of *P. microphyllus* Gray and all its related species represents a comparatively stable stage of development of such reduced form. The reduction in the height of the plant, the size of the leaves, the number of stamens, the length of style and the size of the stigma all conform with the fact of such reduction in number of flowers. Multiplication as well as reduction, and some times a combination of both processes may have taken place in the evolution of the *Philadelphus* inflorescences. The multiplication in the number of

flowers which are produced in the leaf-axils of the succeeding nodes below the terminal one, gives rise to the determinate-racemose type, and further multiplication which involves the branching of the flowering pedicels gives rise to the paniculate type. The mexicanus type is another primitive model which is closely related to the pauciflorous type. The multiplication in the number of flowers and the ramification of the flowering branches of this type give rise to the ramiferous type. The hirsutus type is remote from all other types of *Philadelphus* inflorescence. Its slender pedicels with median or super median bracts, its irregular way of branching, and its appearance remind one of the inflorescence of certain *Deutziae*. It is probably derived from some form very remotely related to the mexicanus type but the linking form is not known in our present flora.

Pedicels: The length of the pedicels in *Philadelphus* varies considerably. The general tendency is, in the determinate-racemose type, the lower ones are longer than the upper ones, or in the pauciflorous types, the lateral ones longer than the central one. As a criterion for classification, this character has little value. Nevertheless, most species have pubescent pedicels. The nature and density of the trichomes on the pedicels of closely related species are sometimes employed as auxiliary characters for recognizing species or varieties.

Hypanthia: Part of the ovary of *Philadelphus* is fused to the receptacle. In this paper the term hypanthium is used to cover that part called the calyx tube by some authors. For the visible top portion of the ovary the term disk is used.

At anthesis, there is no appreciable difference in the shape and size of the hypanthia of closely related species. But the nature and density of the indumentum which persist in the fruit are very useful for specific identifications, or even for the delimitation of series. Most *Philadelphus* species have yellowish green hypanthia. Certain Chinese species have purplish ones. In such case, color may be used as a handy auxiliary character for identifying species or varieties.

Sepals: The sepals of *Philadelphus* are ovate, rarely deltoid, 4 -20 mm. long, acuminate (rarely acute) at the apex. The relatively shortest sepals occur in *P. hirsutus* and the longest ones in *P. inodorus* and *P. mexicanus*. The length, shape and apex of the sepals have been employed by various authors for distinguishing morphologically similar and geographically intermixed species. The study of a large amount of material in this genus reveals that the natural population of any general area belonging to the same section exhibits very little variation in the size and shape of the sepals. Thus, in my opinion, they have no specific significance.

Corolla and petals: Characters of the corolla and the petals have been little used in the classification of the genus. One Central American species has been recognized for its pubescent petals, while another species of northwestern United States has been characterized by its pointed petals.

In shape and size the petals of various species are rather constant. They may be oblong, elliptic, suborbicular or lanceolate. The variations in the shape and size of the petals give the different appearance of the flowers.

Thus *P. inodorus* var. *laxus* (Schrader) S. Y. Hu has oblong petals, and its flowers are distinctly cruciform when fully open (Pl. III, col. 3). The petals of *P. inodorus* Linn. var. *grandiflorus* (Willd.) Gray are suborbicular, and consequently its flowers appear disciform (Pl. III, col. 1). is an important aspect for distinguishing varieties and garden forms, the of *Philadelphus*. It shows a considerable difference in the size, shape and appearance of the corollas in the genus. As the appearance of flowers is an important aspect for distinguishing varieties and garden forms, the size and shape of the petals may eventually have a more important role in demarcating entities subordinate to the species.

Stamens: There is noticeable variation in the number of stamens not only between different species or different plants which clearly represent a single species, but also between different flowers of the same plant. The forms possessing the most stamens are found in *P. inodorus* Linn. and its varieties where as many as 90 stamens have been observed. The smallest number of stamens observed is in *P. mearsnii* Evans where as few as 13 stamens have been counted. But variations in the number of stamens between different flowers on the same plant do exist. With the first cited example as few as 60 stamens and with the second species as many as 20 stamens have been observed. For demarcating morphologically closely related and geographically inseparable species the number of stamens does not seem to have much significance. But there apparently exists a general pattern of stamen number between morphologically different and geographically widely separated groups. Thus the native population of *Philadelphus* of the Southern Appalachian region with pauciflorous inflorescences have the highest stamen count which is between 60 and 90; the xerophytic plants of the southern Rockies with the pauciflorous type of inflorescences have an average count of 30 to 40, rarely as low as 24 or as high as 50 stamens; the native species of Central America with ramiferous inflorescences have 40 to 50 stamens and those with the mexicanus type of inflorescences have 36 to 44 stamens. The Old World species with racemose inflorescences generally have 25 to 35, rarely to 50 stamens. Garden hybrids usually have low stamen counts, and many of them are sterile, with the exception of one form, which has up to 60 stamens, they have 20 to 29, rarely up to 40 stamens. The species with the hirsutus type of inflorescences have the lowest stamen count, ranging 13 to 33. Such a general pattern when correlated with the form of buds, the type of inflorescences and the shape of fruits and the tails of the seeds, may serve as auxiliary criteria for characterizing sections or series of the genus.

Hitchcock was the first person who observed the tendency of the union of the lower portions of the filaments of several adjacent stamens into bundles in *P. argenteus* Rydb. (Pl. IV, fig. 8c), and used this character for distinguishing that xerophytic taxon. Normally the filaments of *Philadelphus* are separated. They are always shorter than the petals. With the exception of the extreme xerophytic dwarf forms like *P. serpyllifolius* Gray or *P. mearnsii* Evans, which has very small flowers and

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short stamens, the length of the filaments in *Philadelphus* is rather constant, with the longest outermost ones being 6–9 mm. long and that of the shortest innermost ones 2–3 mm. long. In the xerophytic forms, the filament of the outer stamens measures up to 4 mm. long and the inner ones 2 mm. long. So far as I know, the longest filament of *Philadelphus* is found in a garden form called *P.* "*slavini*" hort ex Wymn. with the inner filaments 7 mm. and the outer ones 12 mm. long. The filaments of *Philadelphus* have not and very likely never will furnish outstanding characters for distinguishing taxa of any rank in the classification of the genus.

The anthers of *Philadelphus* are generally oblong, being 1–1.2 mm. long, 0.9 mm. wide. The xerophytic species like *P. serpyllifolius* Gray has subglobose anthers, 0.5 mm. in diameter. There are a few natural populations occurring in Central China and western North America where hair-like processes occur on the thecae of the anthers (Pl. IV, fig. 8c). This is probably an expression of an unusual mutation which eventually may lead to speciation.

Pistil: A normal pistil of *Philadelphus* is composed of four carpels. Occasionally few 5-carpelled or very rarely some 3-carpelled pistils may occur in a garden form. Characters furnished by the parts of the pistil, ovary, style, and stigmas, have been employed for distinguishing taxa of various rank in *Philadelphus*. Schrader recognized *P. speciosus* for its 8-loculed fruit. Pursh distinguished his *P. lewisii* for its relatively long and much divided style. Koehne subdivided the major groups of the genus on the basis of the size of the stigma. Ruprecht, Koehne and many others have proposed species because of the presence of hairs on the style, or disc, or both. Nevertheless, due to our limited knowledge of the pistil in *Philadelphus* unnecessary binomials have been created. A normal *Philadelphus* ovary has four locules and an axile placentation. In each locule there are a pair of more or less fused auricular placentas projecting from the upper portion of the central column (Pl. I, fig. 10–12). The superior lobes of these placentas are much shorter than the inferior ones, the latter are so pressed together that they appear as one organ in cross sections (Pl. I, fig. 10B). In *P. inodorus* Linn., its varieties, and its related species, the inner wall of the roof of each locule, which corresponds

PLATE III

FLOWERS OF PHILADELPHUS CULTIVATED IN THE ARNOLD ARBORETUM SHOWING DIFFERENT FORMS OF THE COROLLA, THE READING IS BY THE COLUMNS 1, 2, 3, AND 4, EACH FROM THE TOP TO THE BOTTOM:
COLUMN 1. P. "Argentine," *P. grandiflorus*, *P. caucasicus*, *P. coronarius* "*speciosissimus*," *P. coronarius*, var. *primulaeflorus*, *P. coronarius*; COLUMN 2. *P. insignis* (?), *P. incanus*, *P. falconeri*, *P. floridus*, *P. delavayi*, *P.* "*Cole Glorious*"; COLUMN 3. *P.* "*Belle Etoile*," *P. satsumanus*, *P. lemoinei*, *P. laxus*, *P. magdalenae*, *P. splendens*; COLUMN 4. *P. maximus*, *P. sericanthus*, *P. tenuifolius*, *P. pekinensis*, *P. nepalensis*, *P.* "*bicolor*"; COLUMN 5. *P.* "*Favorite*," *P. virginalus*, *P.* "*Norma*," *P. zeyheri*, *P. tomentosus*, *P. purpurascens*.

to the upper portion of the middle of the carpel, grows down and projects between the superior lobes of the placentas in such a manner that it appears like a false septum separating those lobes. Thus the cross sections made through the upper portion of a normal 4-locular ovary of such species appear 8-chambered (Pl. I, fig. 10D). This was perhaps what Schrader saw in *P. speciosus*. The position of the attachment of the placentas on the central column affects the shape of the fruit and the length of the tail of the seed. In *P. inodorus* Linn. the placentas are attached above the insertion of the sepals. Consequently the fruits are ellipsoid with circumferential sepals. These fruits have long-tailed seeds (Pl. I, fig. 10). On the other hand, the placentas of *P. microphyllus* Gray are attached about the same level as the insertion of the sepals (Pl. I, fig. 11). The fruits are ellipsoid with supermedian persistent sepals, and the seeds are short-tailed. In *P. hirsutus* Nutt. the placentas are attached below the insertion of the sepals (Pl. I, fig. 12). The fruits are obconic with apical persistent sepals and the seeds are ecaudate. This correlation of the attachment of the placentation, the shape of the fruits and the length of the tails of the seeds indicate that the position of the placentas can be used as auxiliary criteria for the delimitation of subgenera or sections of *Philadelphus*.

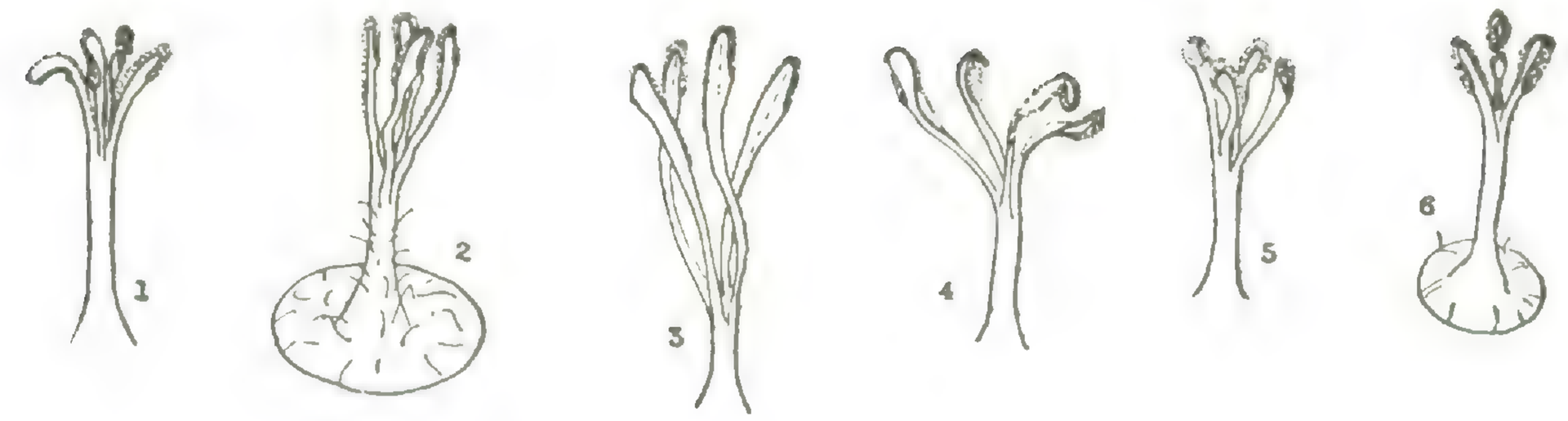
The length and the degree of the union of the style, the number and shape of the stigma and the indumentum of the style and disc have all been used in the classification of *Philadelphus*. Michaux in 1803 in distinguishing *P. inodorus* Linn. from *P. coronarius* Linn. introduced the relative length of the style and the stamens and the degree of union of the style. Since then Pursh has characterized *P. lewisii* as a species with three stigmas and a 3-parted style as long as the stamens, and Nuttall has characterized his *P. hirsutus* as a species with clavate undivided 4-grooved stigma and a style shorter than the stamens. Fortunately the species that Michaux, Pursh and Nuttall dealt with each represents a phylogenetically unrelated group, and incidentally the character holds true for distinguishing them. Later authors including Rydberg and Rehder have used the same character for delimiting closely related species, varieties and garden forms which present varied degrees in the union of the styles. *Philadelphus microphyllus* Gray has been treated as a species with united stigma. But flowers of different collections exhibit varied degree of the union of the styles. Some are completely united, some are partially united and others are completely separated (Pl. IV, fig. 8a, b, e, f). This happens also in *P. argyrocalyx* Wooton (Pl. IV, fig. 9 A-b). So far as I know there is a variation in the degree of the union of the style in every natural population. For this reason such characters fail to be of value for distinguishing species or taxa of lower rank.

There are certain morphological differences existing in the styles and stigmas of geographically separated groups, which, when correlated with characters as the position of buds and the type of inflorescences, may be used as auxiliary criteria for demarcating series or sections. The styles of the southern Mexican species may be long or short, but they all have

elongated cristate stigmas with the fertile papillose surfaces situated largely on the elevated abaxial sides (Pl. IV, fig. 13–15). The styles of the southern Appalachian species with pauciflorous inflorescences are relatively long. They carry oar-shaped stigmas with adaxial as well as abaxial fertile papillose surfaces, the latter though definite in outline, are shorter (Pl. IV, fig. 12). The styles of the Old and the New World species with determinate-racemose inflorescences are comparatively long with clavate or linear stigmas. The fertile surfaces of these stigmas, with the exception of some Yunnan and Japanese species, are longer on the adaxial sides than on the abaxial sides (Pl. IV, fig. 1–6). The styles of the New World xerophytic species with pauciflorous inflorescences are relatively short with linear stigmas, the fertile surfaces of which are largely on the abaxial sides (Pl. IV, fig. 8–9). The styles of the New World species with the hirsutus type of inflorescences are columnar with subcapitate 4-grooved stigmas (Pl. IV, fig. 16–17).

The presence or absence of hairs on the disc and style is a definite and easily recognizable character which may safely be used in the identification of species. Ruprecht in 1857 first used such a character for *P. schrenkii*, Koehne later described *P. lancifolius* from Sikkim, *P. karwinskyanus* from Mexico, *P. subcanus* from Central China and *P. caucasicus* from western Asia on the strength of the same character. Rydberg in 1905 employed this character as the principal criterion in his key. But as abundant material is available for a comparative study of the natural populations of various regions this character is probably not as important as earlier taxonomists considered it to be. In nature among closely related taxa in all regions, there are paired species which differ chiefly in the absence or presence of hairs on the style, disc or both. For example, there are the *P. coronarius* and *P. caucasicus* in southern Europe and western Asia, *P. tenuifolius* and *P. schrenkii* in northeastern Asia, *P. subcanus* and *P. incanus* in Central China, *P. satzumi* and *P. lasiogynus* in Japan, *P. lewisii* and *P. gordonianus* in northwestern United States, *P. stramineus* and *P. pumilus* in southwestern United States, *P. pubescens*, and *P. gattingii* in southeastern United States, and *P. coulteri* and *P. asperifolius* in Mexico. It is not impossible that such phenomena merely represent an expression of normal Mendelian inheritance of one character. But our knowledge of the genetics of these groups is lacking. For the present, and in the absence of cytogenetic information, the presence or absence of hairs on the disc, style, or both is retained for the purpose of distinguishing certain manifestly closely related taxa.

Capsules: The fruit of *Philadelphus* has not been used to any extent in the classification of its various taxa. The material that I have examined apparently presents subgeneric or at least sectional differences in the shape of the capsules and the position of their persistent sepals. The southeastern Mexican species all possess ellipsoid or obovoid fruits with median sepals while the northeastern Mexican species have globose fruits and subapical sepals (Pl. IV, fig. 26–28). The pauciflorous species have ellipsoid fruits and median persistent sepals while the species of the same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area possessing the hirsutus type of inflorescences have obconic fruits with apical persistent sepals (Pl. IV, fig. 25). The position of the persistent sepals may be used as a satisfactory auxiliary criterion in distinguishing morphologically close but geographically remote species. *Philadelphus lewisii* Pursh and *P. pekinensis* Rupr. both have pseudoracemose inflorescences and glabrous hypanthia. Besides the geographical separation, the subapical sepals attached to the fruit of the former and the apical ones

PLATE IV

THE STYLE AND STIGMA OF *Philadelphus* (all × 2½). 1. *P. coronarius*, the stigmas slightly enlarged, the abaxial surface definite, shorter than the adaxial. 2. *P. caucasicus* with pubescent style and disk. 3. *P. coronarius* var. *duplex* (Kew 1307); the stigmas broadened. 4. *P. tomentosus*, the adaxial surface split into two. 5. *P. pekinensis*, the abaxial surfaces much shorter than the adaxial. 6. *P. kansuensis*, the stigmas often 3, the disk with few hairs, the abaxial surface much longer than that of *P. pekinensis*. 7. *P. delavayi*, a. and c. from Yunnan (*Feng 1012*), b. from Latong, Tibet (Younghusband). 8. a–b and d–f. *P. microphyllus* with the styles separated in various degrees, the fertile surface of the stigma abaxial (a. *Ellis 107*, b. *Eggleston 18654*, d. *Heller 3792* and f. *Alexander-Kellogg 1785*). 9. *P. argyrocalyx* with the stigmas separated or united (a. *Eggleston 14541*, b. *Wooton* in 1895). 10. *P. argenteus* with the style slightly separated (*Mearns 1617*). 11. *P. inodorus* with oar-shaped stigmas, the abaxial surfaces broadened, shorter than the narrow adaxial surfaces (*AA15347*). 12. *P. "bicolore"* with elongated style and enlarged stigmas (*Hu* in 1951). 13. *P. affinis*, the style long and hairy, the stigmas elongated with few hairs on the sterile portion (*Berlandier 333*). 14. *P. calcicolus* with the stigmas more or less united, broadened and cristate, the style short, glabrous (*Meyer & Roger 2662*). 15. *P. karwinskyanus* with the stigmas cristate and hairy on the sterile portion, the style short and pubescent. 16. *P. hirsutus* with the style comparatively long, the stigmas clavate and undivided, the stigmas on 4 ridges. 17. *P. serpyllifolius* with the style short, the stigmas undivided and subcapitate.

FRUIT OF *Philadelphus* (× 1). 18. *P. tenuifolius* with the apical end rounded (*Cen. 263*). 19. *P. tomentosus* with the apical end pointed and the persistent calyx almost circumferential (*Parker*, in 1919). 20. *P. sericanthus* with the apical end rounded, the lower portion pubescent. (*Steward, Chiao & Cheo 609*). 21. *P. pekinensis* with very small fruit (*King 626*). 22. *P. inodorus* with ellipsoid fruit. 23. *P. argyrocalyx* with subglobose fruit, the lower portion lanate (*Rehder 315*). 24. *P. hirsutus* with flat apical end (Biltmore Herb. *4333*). 25. *P. hitchcockianus* with very small top-shaped fruit which is broader than long (*Moore 3477*). 26. *P. sargentianus* with subglobose fruit (*Pringle 2094*). 27. *P. karwinskyanus* with ellipsoid fruit pointed at both ends (*Rose & Hough 4412*). 28. *P. mexicanus* with obovoid fruit the lower portion 4-angled. 29. Cross-section of the fruit of *P. mexicanus*, one third from the base.

SEEDS OF *Philadelphus* (× 10). 30. The short-caudate seed of *P. pekinensis* with round-lobed crown. 31. The long-caudate seed of *P. inodorus* with pointed-lobed crown. 32. The short-caudate seed of *P. californicus*. 33. The ecaudate seed of *P. hirsutus*.

SOME UNUSUAL STAMENS OF *Philadelphus*. 8c. Stamens with fused filaments (*Eggleston 18654*). 8g. Stamen with hirtellous anther (*Abram 7200*).

to the fruit of the latter are outstanding characters for distinguishing these species.

Seeds: Seeds are minute in all species of *Philadelphus*. Each individual seed consists of a small ellipsoid body about 1–2 mm. long wrapped in a thin testa extending towards both ends. The large portion of this small body is the copious oily endosperm which imbeds the microscopic embryo. The hypocotyl and the radicle constitute two-thirds of the embryo proper. The cotyledons and the epicotyl are very minute. The testa is reticulate, light brown, castaneous, or rarely black. It extends into an irregular collar-like crown at the proximal end and a tail-like wing at the distal end. The crowns of the seeds of different species vary in shape. That of the seed of *P. pekinensis* Rupr. has more or less rounded lobes (Pl. IV, fig. 30), that of the seed of *P. inodorus* Linn. has pointed lobes (Pl. IV, fig. 31), and that of the seed of *P. hirsutus Nutt.* is very minute and inconspicuous (Pl. IV. fig. 33). The length of the seed-tail varies as well as the shape of the crown. *Philadelphus inodorus* Linn. has a long-tailed seed, *P. pekinensis* Rupr. has a short-tailed seed and the seed of *P. hirsutus* Nutt. has no tail. Seed characters have never been used in the classification of *Philadelphus*. The shape of the crown and the length of the tail of the seed correlate with the position of the buds, the type of the inflorescence, and the form of the stigma. In my opinion they are characters of subgeneric or sectional importance. In some cases they can be used to distinguish intricate species. For example, because of the superficial similarities of the leaves and the corollas of *P. lewisii* Pursh and *P. californicus* Benth. and also because of their overlapping geographic distribution, some botanists have placed the latter as a variety of the former. As *P. lewisii* Pursh has long-tailed seeds and *P. californicus* Benth. has short-tailed seeds (Pl. IV. fig. 32), and as this character is associated with the difference in the inflorescences, *P. californicus* Benth. should be considered as a good species.

In summarizing the study of the gross morphology of *Philadelphus*, it seems legitimate to conclude that characters such as the dichasial inflorescence, large number of stamens, elongated stigma with enlarged papillose fertile surface, high insertion point in the placentation, ellipsoid fruit with circumferential calyx lobes, and long-tailed seed can be interpreted as primitive ones, while in contrast, characters like solitary flower, the racemose or paniculate inflorescence, the small number of stamens, the reduced length of the stigma, the low point of insertion in the placentation, the obconic fruit with apical persistent sepals and the short-tailed seed can be interpreted as representing more advance stages in the evolution of the genus.

SUBDIVISIONS OF THE GENUS AND THE PHYLOGENY OF ITS MAJOR GROUPS

Based on the data found in the position of the buds, in the type of inflorescences, in the form of stigmas, in the shape and position of the persistent sepals on the fruits, and the nature of the seeds, I am arranging

the species of *Philadelphus* into four subgenera and nine sections. The characters of these taxa are stated in the following synopsis.

SUBGENUS I. **Gemmatus**: This subgenus includes all the species with exposed buds; depauperate paniculate inflorescences, one or three terminal flowers with jointed pedicels or many flowers in ramified branchlets; stamens 40–60; semi-inferior ovary, enlarged and often cristate, separated stigmas; obovoid-ellipsoid or subglobose fruits with circumferential sepals; and long-caudate seeds. It contains 14 species in two sections.

SECTION 1. **Poecilostigma**: Inflorescences compound, 1- up to many-flowered; stamens 40 to 50; stigmas elongated and cristate; fruits obovoid-ellipsoid; southeastern Mexico, Guatemala to Costa Rica.

SECTION 2. **Coulterianus**: Inflorescences with solitary flowers, rarely 3-flowered; stamens 30–44; stigmas elongate, not cristate; fruit subglobose; northeastern Mexico.

SUBGENUS II. **Euphiladelphus**: This subgenus includes all the species with enclosed buds, determined branches, determinate-racemose or pauciflorous inflorescences, large or medium number of stamens, clavate or oar-shaped or linear stigmas, and long- or short-tailed seeds. It comprises 41 species in three sections.

SECTION 3. **Pauciflorus**: Inflorescences true dichasial cymes, often reduced to one or three flowers; stamens 60–90; stigmas oar-shaped; fruit ellipsoid with circumferential sepals; seeds long-tailed with pointed lobes on the crown; two species, native of the Southern Appalachian region of the United States.

SECTION 4. **Stenostigma**: Inflorescences determinate-racemose; stamens 25–35, rarely over 40; stigmas clavate or linear; fruit ellipsoid with subapical persistent sepals; seeds long- or short-tailed, the crown with pointed or rounded lobes; 30 species in both the Old and the New Worlds.

SECTION 5. **Microphyllus**: Inflorescences pauciflorous; stamens 25–40, rarely up to 50, stigmas linear; fruit ellipsoid with circumferential or subapical persistent sepals; seeds short-tailed with rounded lobes on the crown; 11 species, Colorado Plateau, Mexican Highland, and northern Mexico.

SUBGENUS III. **Marcrothyrsus**: This subgenus includes species with exposed buds; determined branches, paniculate inflorescences; medium number of stamens; clavate stigmas, and short-tailed seeds. It has one section including three species, native of California.

SECTION 6. **Californicus**: Characters as the subgenus.

SUBGENUS IV. **Deutzioides**: This subgenus includes all the species with exposed buds, and indeterminate branches; solitary, rarely ternate flowers; 13–35 stamens; inferior ovary, and columnar or subcapitate 4-grooved stigmas; turbinate or subglobose fruits with apical persistent sepals, and ecaudate seeds. It comprises eight species in three sections.

SECTION 7. **Hirsutus**: Flowers ternate; mesophytic plants; leaves serrate, hirsute, hairs all straight, style 4 mm. long; two species, Tennessee, Alabama.

SECTION 8. **Pseudoserpyllifolius**: Flowers solitary; xerophytic, dwarf plants, leaves entire, strigose or strigose-villose, hairs all straight; style up to 1 mm. long; four species, Texas, New Mexico, and Northern Mexico.

SECTION 9. **Serpyllifolius**: Flowers solitary; xerophytic, dwarf plants, leaves entire, lanate and hirsute beneath, trichomes dimorphous; two species, Texas, New Mexico, Arizona, Northern Mexico.

The interrelationship of the subgenera and sections is indicated graphically in the following figure.

In this classification primitive characters such as enlarged stigmas, high point of attachment in the placentation and long-tailed seeds are found both in the section Pauciflorus of the subgenus Euphiladelphus and the section Poecilostigma of the subgenus Gemmatus. The true dichasial inflorescences and the very large number of stamens of sect. Pauciflorus indicate that species in this section retain more primitive characters than those of sect. Poecilostigma which has apparently reduced compound inflorescences and moderate number of stamens. Yet the exposed buds of sect. Poecilostigma and the elongated cristate stigmas of many of its included species show that this section is more primitive in these respects. Morphological evidences, obviously suggest that our present species of *Philadelphus* seem to express two lines of evolution. They probably have originated from a common stock with exposed buds, dichasial inflorescences, exceedingly large number of stamens, and elongated cristate stigmas. Such a hypothetical "Protophiladelphus" does not exist in our present flora. The species of the section Pauciflorus occur in the mesophyllous forest of the southern Appalachian region, and those of the section Poecilostigma are associated with vegetations constituting the same type of forest in Mexico.[1] Apparently species in these two sections have existed for millions of years with very little changes.[2] They both represent very ancient stocks in the development of the genus.

[1] A. J. SHARP, Characteristics of the Vegetation in Certain Temperate Regions of Eastern Mexico. Ecology **31**: 313–333. 1950.

[2] S. A. CAIN, The Tertiary Character of the Cove Hardwood Forests of the Great Smoky Mountains National Park. Bull. of the Torrey Bot. Club **70**: 213–235. 1943; and A. J. SHARP. The relation of the Eocene Wilcox Flora to some Modern Floras. Evolution **5**: 1–5. 1951.

Species of the sect. Stenostigma share the character of enclosed buds with the sect. Pauciflorus. This section with its determinate-racemose inflorescences, moderate number of stamens and some long-tailed but largely short-tailed seeds seems to have derived from the sect. Pauciflorus, the direct link seems to be from the *P. inodorus* type of plant to the *P. lewisii* type of plant. In this process of evolution, the changes involved are: (1) the suppression of the branching of the rachis of the lateral flowers of the true dichasia of the sect. Pauciflorus, thus prohibiting the formation of

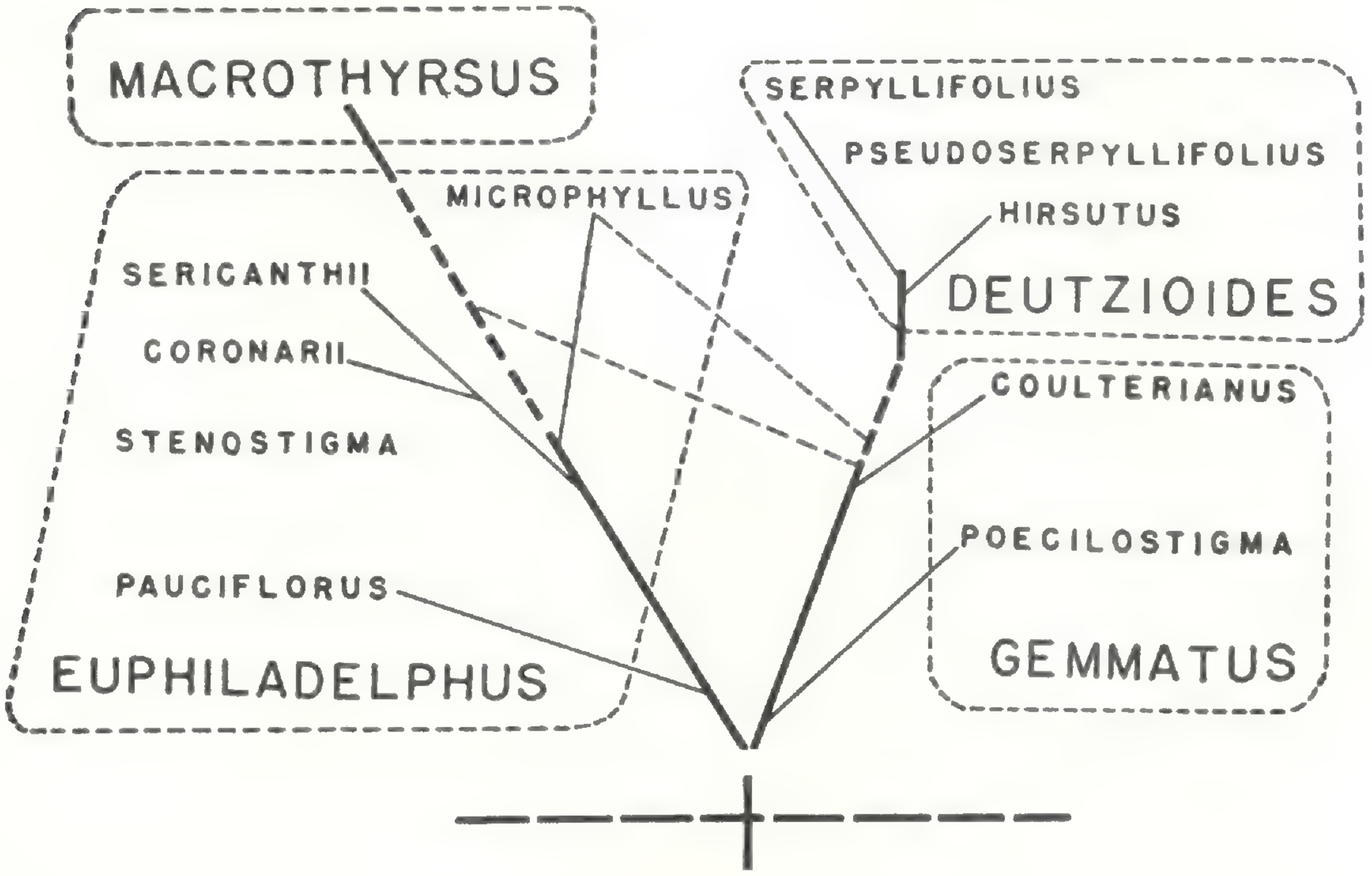

FIG. 1. Relationships of the subgenera and sections of *Philadelphus* as indicated by morphological similarities. The solid lines indicate relative close relationships while the broken lines indicate lesser affinities.

the lateral cymes, (2) certain genetic modifications which promotes the differentiation of the tissue in the shoot apex, so that flower primordia are formed not only at the terminal nodes, but also in the axils of the leaf primordia, and consequently the determinate-inflorescences of the sect. Stenostigma are developed, (3) the reduction of the number of stamens, (4) the narrowing of the stigmatic surfaces, and (5) the lowering of the point of attachment in the placentation. The shortening of the seed-tails represents a more advanced stage of evolution in this section. These changes must have taken place before the Miocene period of geological time for fossil species of *Philadelphus* resembling the present small-leaved forms of *P. lewisii* Pursh existing in the Upper Miocene have been discovered by Chaney in Oregon and Colorado. It is very probable that during the Eocene period when North America, northern Asia and north-

ern Europe supported a temperate and subtropic flora, the species of the section Stenostigma were so well established and so widely distributed on the American and Eurasian continents that they had a holarctic distribution and a transcontinental range. The present disjuncted Old World and New World distribution represents its disturbed range and the existing species of this section may hence be considered as "living fossils" corresponding to the situation of *Sequoia* and *Metasequoia*.

The section Microphyllus culminates the Euphiladelphus line of descent. Its species share the characters of narrow stigmas and short-tailed seeds with the section Stenostigma. The majority of them have small leaves and pubescent hypanthia, characters common to xerophytic species. In the course of the evolution of these species the changes involved are chiefly in the development of the dwarf habit of the plant, in the reduction of the size and the increase in the thickness of the leaves, the formation of dense indumentum and in the suppression of the formation of the axillary flowers. These changes must have taken place at or after the end of the Eocene period when America saw the elevation of the Rocky Mountains. The consequent aridity necessitated such adaptation for xerophytic living.

The subgenus Macrothyrsus, though small in constitution, has a peculiar position in the classification and evolution of *Philadelphus*. On one hand it shares the moderate number of stamens, the clavate stigmas, the medianly attached placentation and the short-tailed seeds with species in the Stenostigma section of the subgenus Euphiladelphus but on the other hand its exposed buds link it to the subgenus Gemmatus. In addition to this peculiar combination of characters its paniculate inflorescence is very unique. It is probably most closely related to the subgenus Euphiladelphus. The general habit, the leaves and the appearance of the individual flowers of its included species, *P. californicus* Benth., resemble those of *P. lewisii* Pursh, a species of the section Stenostigma of the Euphiladelphus, so much that it has tempted botanists to treat it as a variety of the latter species. Apparently this stock has originated from the subgenus Euphiladelphus with a tenuous influence of the section Gemmatus.

The species of the section Coulterianus share the exposed buds and the long-tailed seeds with the Poecilostigma. Apparently this section represents a continuation of the Gemmatus line of evolution. In this stock a general tendency in the adaptation for a more xerophytic habitat is very prominent. It is shown both in the reduction of the size of the leaves and in the increased thickness of the indumentum. The stigmas of this section are elongate but not as a rule cristate, and the fruits are more or less globose in outline. In the size of the leaves, the pubescences of the hypanthia and in the form of the fruits, some species of this section, such as *P. sargentianus* S. Y. Hu express a strong resemblance to *P. argyrocalyx* Wooton of the section Microphyllus of the subgenus Euphiladelphus. These similarities are rather superficial. The gap between these species is wide for they differ in the fundamental criteria as to the position of the buds and the nature of the seeds.

Morphologically the subgenus Deutzioides is only remotely related to *Philadelphus*. In the low point of attachment of the placentation, the obconic fruit and the tailless seeds, this subgenus shows a close affinity to the Asiatic genus *Deutzia*. In fact, the appearance of a branch of *P. hirsutus* Nutt., the type species of the section Hirsutus, resembles that of a branch of *Deutzia grandiflora* Bge. of West China (Szechuan and Yunnan) more than it does of any American species of *Philadelphus*. Nevertheless, the species of this subgenus should not be separated from *Philadelphus* because of the indefinite number of unappendaged stamens and the simple straight hairs. In *Deutzia* the stamens are usually 10 and are always appendaged, that is, the filaments are winged. The trichomes of *Deutzia* are all stellate. The point of origin of this line of evolution in *Philadelphus* is not clear, but evidently it was not from the stock which gave rise to the Euphiladelphus species. The exposed buds of this subgenus indicate its faint affinity with the subgenus Gemmatus. Yet its ecaudate seeds, the columnar styles, and the coalescent stigmas imply a wide gap between them. It seems apparent that in the course of the evolution of *Philadelphus*, there has been a tendency towards the production of Deutzia-like plants. It appears that in the New World the process stopped in the subgenus Deutzioides, while in the Old World the change was more abrupt, the resulting genus, *Deutzia*, once established, diversified more rapidly than *Philadelphus*, and consequently occupies a wider area than *Philadelphus*. This conforms with Professor Sax's finding in the chromosome numbers of the two genera.[1] Accordingly, the basic chromosome number of *Philadelphus* and *Deutzia* are the same, n = 13, but in *Deutzia*, many species are polyploids. The xerophytic taxa of the subgenus Deutzioides may have the appearance of some species of the section Microphyllus. For example, *P. mearnsii* Evans of the section Pseudoserpyllifolius resembles *P. pumilus* Rydb., and *P. texensis* S. Y. Hu of the section Serpyllifolius has the appearance of *P. microphyllus* Gray. But these resemblances are superficial. *Philadelphus mearnsii* and *P. serpyllifolius* have exposed axillary buds, columnar styles, and ecaudate seeds and *P. pumilus* and *P. microphyllus* have enclosed buds, divided styles and short-tailed seeds. These superficially resembled species are developed from different stocks, the separation of which occurred in remote geological times. The exposed buds and the large serrate leaves of *P. hirsutus* Nutt. resemble those of *P. mexicanus* Schlecht. But the low point of attachment in the placentation, the columnar style and the ecaudate seeds of the former species indicate its advanced position on the genealogical tree of the genus. It is legitimate to assume that the representatives of the section Hirsutus were derived from the subgenus Gemmatus early in the evolution of the genus, and developed independently into the present forms. The species of the section Pseudoserpyllifolius are pygmies of this line of development and come about through the reduction in the size of the leaf to meet changed climatic and topographic require-

[1] K. Sax, Chromosome numbers in the Ligneous Saxifragaceae. Jour. Arnold Arb. **12**: 198–204, 1931.

ments characteristic of a xerophytic environment. They are intermediate forms between members of the sections Hirsutus and Serpyllifolius. In indumentum they resemble the former and in size and general appearance they resemble the latter. The species of the section Serpyllifolius represent the climax of this line of evolution.

CYTOLOGY

Investigations of the cytology of *Philadelphus* have been undertaken by W. Bangham in Boston and Janaki Ammal in London. Bangham in 1929 [1] examined the pollen mother cells of 37 species, hybrids and varieties of *Philadelphus* grown in the Arnold Arboretum and concluded that there is no marked difference in the chromosome groups among those taxa. He reported that each species had a diploid chromosome count of 26. He observed that the chromosomes of the hybrids were perfectly compatible and there was no evidence of lagging and other aberrant behavior. His observation on the chromosome behavior of a garden form of *P. pubescens* Loisel., which was then assumed by Rehder to be a cross between *P. tomentosus* Wall. of the Himalayan Region and *P. pubescens* Loisel. of southeastern United States, led him to conclude that there must have been very little change in the chromosome makeup of *P. tomentosus* Wall. and *P. pubescens* Loisel. in the millions of years that they, or their ancestors, have been separated.

Janaki Ammal in 1951 [2] studied the chromosome number and behavior of *Philadelphus* grown at the Royal Botanic Gardens, Kew and the gardens of the Royal Horticultural Society at Wisley, England. She confirmed Bangham's findings that the natural species are diploids with the chromosomes 2n = 26. But her observation of the chromosome behavior of the hybrids differs from that of Bangham. She reported that lagging and other types of aberrant behavior are generally associated with hybridity in *Philadelphus* and consequently give rise to high pollen sterility. In the case of the trispecific hybrids, *P. purpureo-maculatus* Rehd., the chromosome behavior is so irregular that it causes the production of unreduced germ cells. By the fertilization of an unreduced egg cell with a normal pollen, triploid garden forms resulted. She found that *P.* "*Sybille*," *P.* "*Belle Etoile*" and *P.* "*bicolor*" are all triploids. She also observed a newly produced hybrid, *P.* "*Beauclerk*," with tetrasomic diploid chromosome composition, 2n = 28. She thus concluded, "though differences in chromosome number do not exist in nature, there are differences in morphology of the chromosome which interfere with pairing in their hybrids between widely separated species . . . for the first time since Eocene times polyploidy has been induced in a genus which has remained diploid for millions of years in nature, by the bringing together under cultivation

[1] The Chromosomes of Some Species of the Genus Philadelphus. Jour. Arnold Arb. **10**: 167–169. 1929.

[2] Chromosomes and the evolution of Garden Philadelphus. Jour. Royal Hort. Soc. **76**(8) : 269–275. 1951.

and the consequent hybridization of races widely separated geographically."

Bangham worked on plants cultivated in Boston and Janaki Ammal's material was grown in London. These two cities are located out of the natural ranges of the genus *Philadelphus*. The climate of these cities only supports the outdoor growth of a few species and their forms. A close examination of the lists of species studied by Bangham and Janaki Ammal reveals that they covered very limited portions of the geographically widely spread and morphologically much diversified genus. Thus it appears to me that the cytological investigation of the natural species is not inclusive enough for any cytologist to draw a conclusion as to whether differences in the chromosome number of *Philadelphus* do exist in nature or not. A large scale transplanting of natural species from southeastern and western United States and Central America into gardens situated in areas warmer than Boston or London, such as the United States National Arboretum in Washington, D. C. or the Boyce Thompson Southwestern Arboretum for the study of the drought resisting species, will doubtlessly provide better opportunities for more exhaustive cytological studies of the genus and advance our knowledge of the cytotaxonomy in this group.

GEOGRAPHIC DISTRIBUTION

The subgenus Gemmatus with its exposed axillary buds, simple, reduced or ramiferous thyrse, high point of attachment in the placenta, broadened usually cristate stigma and long-tailed seeds, represents morphologically, I feel, the more primitive elements of the genus. The species are largely subtropical or tropical in distribution. They are limited to the New World, with eastern Mexico being its center of concentration. The range extends ten degrees toward the north and the south of the Tropic of Cancer. The effect of rainfall, temperature, altitude and latitude on the distribution of the different species of this subgenus in Mexico is very evident. *Philadelphus karwinskyanus* is found only on the Great Cross Range and hence westward along the Pacific Coast at lower altitudes where the climate is warmer. In the warm and humid section of the Sierra Madre Oriental, one finds *P. affinis* with its subglabrous hypanthium. At higher altitudes of the same range grows the small-flowered *P. asperifolius*. Hence northward into the arid northeastern Mexico, occur various endemic species belonging to the Section Coulterianus. In the neighborhood of the Tropic of Cancer at high altitude where the rainfall is low, *P. maculatus*, a small-leaved form with reddish purple spot at the base of each petal, grows.

The true *P. mexicanus* with its solitary or ternate flowers and pubescent petals occurs only on the Sierra Madre del Sur, the southern area of the Sierra Madre Oriental, and in Chiapas, hence southwestward to Guatemala. In southern Mexico and Guatemala, a species with pubescent petals and ramiferous inflorescences, *P. myrtoides,* occurs. This species extends southward to the Province of Chiriqui in Panama, the southern limit of the range of distribution in the genus.

The subgenus Euphiladelphus includes geographically the more widely distributed elements. Its representatives occur in Europe, Caucasus, the Himalayan region, China Proper, Manchuria, Japan, a large part of the United States, and adjacent southwestern Canada and northeastern Mexico. It is an assemblage of species adapted to the climatic conditions of the North Temperate Zone, between latitudes 25–50° N. in both the Old and the New World.

In the Old World, the subgenus is rather stable. Radical changes did not occur in the course of its evolution. All the Old World species belong to one section, Stenostigma. In Europe, it is represented by *P. coronarius* which occurs, according to Hegi, spontaneously in Romania, Austria and southern Germany. In the Caucasus Mountains, it is represented by *P. caucasicus,* a species which differs from *P. coronarius* only in its pubescent discs and styles. The eastward distribution of the section is interrupted in Central Asia. No species is met with until it reaches the Himalayan Mountains. There the species concentrate in Sikkim, Nepal and eastern Punjab where it is represented by *P. tomentosus* and its related forms. In China more marked morphological changes were involved in the course of the evolution of this group. There the section can be subdivided into several series. The Tsingling Range seems to provide a central stage from where the different lines of evolution in the species can be traced. At the western end of this mountain range occurs *P. kansuensis*, a species having the leaf character of *P. pekinensis*, a North China element, the pubescent disc of *P. subcanus*, a Central China element and the pubescent hypanthium of *P. henryi*, a southwestern China element. At the eastern end of this mountain range, occurs *P. sericanthus* and its related forms. South of this range grows *P. purpurascens*, an intermediate form between the Tsingling and the Yunnan species, *P. delavayi.* The latter species morphologically and geographically links the Chinese and the Himalayan elements. North of the Tsingling Range in Shansi, Shensi and Kansu occurs *P. laxiflorus*, a species morphologically and geographically intermediate between *P. pekinensis* and *P. sericanthus*. The northernmost limit of the distribution of this section in the Old World is the wooded valley of the Amur River and its tributaries, the Sungari and Ussuri rivers in Manchuria, where it is represented by *P. tenuifolius* and *P. schrenkii.* These species also occur in Korea. In Japan this subgenus is represented by *P. satsumi* and its related forms.

The distribution of *Philadelphus* in Eastern Asia presents a very interesting phytogeographic phenomenon, that is, the complete absence of the genus from the flora of Taiwan (Formosa). It is a well known fact that Taiwan and Yunnan have very pronounced floristic affinities. Many species as well as genera that occur in one province are also present in the other. But in the case of *Philadelphus*, the genus is abundant in northwestern Yunnan and is completely absent from Taiwan. This fact may be taken as an indicative factor for confirming our belief as to the origin of the genus and for explaining the pattern of its distribution in Eastern Asia. The genera and species that are common to Taiwan and

Yunnan are of Old World origin. *Philadelphus* is obviously of New World origin, and its distribution in Eastern Asia seems to have been southward in direction. Apparently neither the Japanese elements nor the continental Chinese elements of this genus reached Taiwan in their migration.

In the New World, the subgenus Euphiladelphus is much more diversified, and consequently three sections are represented. Two of these three sections, Pauciflorus and Microphyllus, are endemic to the United States. Few species of the section Microphyllus also occur at the northern border of Mexico. The third section, Stenostigma, America shares with Europe and Asia. In North America the species of the section Stenostigma can be subdivided into two series the Gordoniani and the Pubescentes. Species belonging to the Gordoniani series occur along the Snake and Columbia Rivers, hence southward reaching the mountains of the California Coast Range. Among the wild population, there seems to be two elements, *P. lewisii* with a glabrous hypanthium and *P. helleri* with a slightly pubescent hypanthium. Morphologically there seems to be little distinction between them, other than the presence or absence of the hairs on the hypanthium, but ecologically there are certain differences. In the natural population of the general area considered, I have examined 292 individual collections totaling 361 sheets. Of these, 177 have glabrous hypanthia and 115 have slightly pubescent ones. After plotting the localities of these collections on a map and then superposing this figure on Rehder's map of climatic zones,[1] a rather striking fact is revealed. Over 77% of *P. lewisii* occur in zones where the average annual minimum temperature is — 10° to — 5° F. while over 47% of *P. helleri* occur in zones where the average annual minimum temperature falls to — 20° to 10° F. The checking also indicates that the center of distribution of *P. lewisii* is in the lower valley of the Columbia River and in the northern portion of the Pacific Border Province while *P. helleri* occurs largely in the intermontane basin and the deeply dissected mountain uplands of the northern Rocky Mountains. Species belonging to the series Pubescentes occur in the Ozark Plateau and the Arkansas Valley of the Interior Highlands and the Interior Low Plateau region of Tennessee, Kentucky, and southern Ohio.

The section Pauciflorus with dichasial inflorescences, very large number of stamens, enlarged stigmas, and high point of attachment in the placentation and long-tailed seeds, retains all the primitive characters of the genus. Species of this section concentrate in the mesophyllous forest of the southern Appalachian region with the periphery of their range reaching the Coastal Plain region along the borders of Georgia and Alabama in the south. It seems that species of this section are rather inactive geographically and stable morphologically, for with all the material I have examined, there are very slight variations.

The section Microphyllus includes the xerophytic species. Its range covers the southern Rocky Mountains in Central Colorado, the Colorado Plateau in western Colorado, Utah, northern New Mexico and Northern Arizona, the Sonoran Desert region in southern Nevada and southeastern

[1] Man. Cult. Trees, Shrubs pp. xii–xiii, 1940.

California and the Mexican Highland in Eastern Arizona, southwestern New Mexico and western Texas, and the adjoining Mexico. In this large semidesert or desert area the populations are localized and isolated. There are many endemics.

The subgenus Deutzioides is strictly a North American taxon. Its three sections occur in two different floristic provinces. The section Hirsutus, as represented by *P. hirsutus* Nutt. and its related forms, concentrates in the mesophyllous forests of the Southern Appalachian Mountain areas with the Tennessee River and its tributaries being the center of its range. The other two sections, Pseudoserpyllifolius and Serpyllifolius, are constituted of xerophytic species which occur in southwestern Texas, New Mexico, southern Arizona, and northern Mexico. It seems that the Mexican Highland is a meeting ground of different elements, the subgenera Euphiladelphus from the north, Deutzioides from the east and Gemmatus from the south.

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Syringa Adanson, Fam. Pl. **2**: 244. 1763. — Moench, Meth. Pl. 678. 1794, non Linn. 1753.

TYPE SPECIES: *P. coronarius* Linn.

Flowers solitary, ternate, in determinate racemes or in depauperate panicles, generally fragrant. Calyx-tubes turbinate or subcampanulate, adnate to the ovary forming the hypanthia, glabrous or pubescent, the

sepals 4, rarely 5, ovate, acute or acuminate; corolla white, rarely with purplish center, the petals 4, rarely 5, in cultivated forms often doubled; stamens 13–90, epigynous, the filaments subulate, free, rarely several united at the base, the anthers oblong, rarely subglobose, glabrous, rarely pilose; ovary inferior or semi-inferior, 4-, rarely in anomalous forms 5-locular, the styles 4, rarely 3 or 5, entirely connate, partially free or rarely in some cultivated forms entirely free, the stigmas free and linear, clavate, oar-shaped, cristate, or coherent and columnar or subcapitate; placentas auriculate, projected from the upper portion of the central axis; ovules numerous, multiseriate, imbricate, pendulous. Capsules ellipsoid, turbinate, hemispherical or subglobose, corticate, the cortex chartaceous, the pericarp cartilaginous, loculicidal. Seeds oblong-subcylindric, the testa brown or nigrescent, membranous, reticulate, generally extending anteriorly into a fimbriate white crown and posteriorly into an obtuse or acuminate tail, the funiculus nigrescent, persistent, the embryo minute, embedded in the carnose and oily endosperm. Shrubs, erect, arching, subscandent or rarely subspinescent; branchlets opposite. Leaves opposite, deciduous, rarely evergreen, serrate or entire, triplinervate or quintuplinervate, glabrous or pubescent, the hairs simple, rarely evergreen, exstipulate; axillary buds exposed or enclosed.

The generic name, Philadelphus, is derived from the Greek root φιλος meaning love, δελφος meaning brother. It was originally used by the ancient Greeks, said to be named for Ptolemy Philadelphus, king of Egypt, 283–247 B. C., for some plant the identity of which is now unknown. Many pre-Linnaean authors called the plants which we now ascribe as Philadelphus, "*Syringa alba.*" Clusius [1] named his illustration of the plant *Frutex coronarius*. Bauhin was the first man who interpreted the pre-Linnaean "Syringa alba" as the *Philadelphus* of the Greeks.[2] When Linnaeus established the genus, he adopted Bauhin's concept. The vernacular names occurring in various literatures are enumerated in the following list:

English:	Syringa; common syringa; mock-oranges (for the odor of the flower); pipe tree; pipe privet
French:	Syringa odorant
German:	Pfeifenstrauch; wilder jasmin; falscher jasmin
Dutch:	Witte syring
Chinese:	T'ai-ping-hua = flower of peace; san-mei-hua = mountain mume flower; Mi-tsai = rice fuel.
Spanish:	Geringuilla
Russian:	Tschubuschnik; pustoryl
Central American:	Mosqueta; Acuilotl = water vine; cozticacuilotl; cozticacuilotl xochitl; azahar

[1] Rariorum Plantarum Historia 1: 55. 1601.
[2] Pinax Theatri Botanici 399. 1623.

KEY TO THE SUBGENERA AND SECTIONS.

A. Axillary buds exposed.
  B. Seed long-caudate; stigmas free, broadened, usually cristate; flowers solitary, ternate, or in depauperate panicles; fruit obovoid or subglobose, with circumferential persistent calyx. . . Subg. I. GEMMATUS.
    C. Leaves acuminate, rarely acute; flowers in a depauperate panicle, 1- up to many-flowered, each on a pointed pedicel; the stigmas broadened, cristate; fruits obovoid-ellipsoid . . . . . Sect. 1. POECILOSTIGMA.
    CC. Leaves acute or obtuse; flowers solitary or ternate; the stigma elongate but in general not cristate; fruit subglobose . . . . . Sect. 2. COULTERIANUS.
  BB. Seeds short-caudate; stigmas free, clavate; flowers in panicles of thyrsus; fruit ellipsoid with subapical persistent calyx. . . . . Subg. III. MACROTHYRSUS (Sect. 6 CALIFORNICUS)
  BBB. Seeds ecaudate; stigmas connate, columnar or subcapitate; flowers solitary or ternate; fruit turbinate or subglobose, with apical persistent calyx . . . . . Subg. IV. DEUTZIOIDES.
    C. Leaves hirsute or strigose, all hairs straight.
      D. Style 3–4 mm. long; subscandent shrubs; leaves serrate . . . . . Sect. 7. HIRSUTUS.
      DD. Style 1 mm. long; subspinescent shrubs; leaves entire . . . . . Sect. 8. PSEUDOSERPYLLIFOLIUS.
    CC. Leaves strigose and lanate beneath; style 1–2 mm. long; subspinescent or small slender shrub . . . . Sect. 9. SERPYLLIFOLIUS.
AA. Axillary buds enclosed . . . . . Subg. II. EUPHILADELPHUS.
  B. Flowers solitary, ternate or in dichasial cymes.
    C. Large arching shrubs; stamens 60–90; stigmas free, oar-shaped; leaves 4–10 cm. long. . . . . Sect. 3. PAUCIFLORUS.
    CC. Erect low shrubs of compact growth or spinescent xerophytic bushes; stamens 35–50; stigmas free or partially connate, linear; leaves 0.5–2.5, rarely up to 3 cm. long. . . . . Sect. 5. MICROPHYLLUS.
  BB. Flowers in determinate racemes . . . . . Sect. 4. STENOSTIGMA.

Subgenus I. **Gemmatus** (Koehne), stat. nov.

Philadelphus subg. I. **Gemmatus** (Koehne), stat. nov.

Philadelphus Reihe 4. *Decorticatae pauciflorae* Koehne, Deutsche Dendr. 180. 184. 1893, pro parte.

Philadelphus sect. 1. *Poecilostigma* subsect. 1. *Gemmati* Koehne in Gartenfl. **45**: 450. 1896, pro parte; et in Mitt. Deutsche Dendr. Ges. **1904**(13): 77. 1904. — Engler, Pflanzenf. ed. 2, **18a**: 191. 1930.

TYPE SPECIES: *P. mexicanus* Schlechtendal.

Flowers solitary, ternate, or in depauperate panicles; hypanthia obconic, or subglobose, generally dense pubescent; stamens about 40, rarely more or less; ovary semi-inferior, the stigma distinct, broadened or cris-

tate; capsules obovoid-ellipsoid or subglobose, the persistent calyx circumferential or subcircumferential; seeds long-caudate, the crowns with pointed lobes, erect or subscandent shrubs or vines; leaves evergreen or deciduous, remotely denticulate or serrate, triplinervate or quintuplinervate; petioles often twisted; axillary buds exposed.

This subgenus is strictly a Central American taxon. In the southern portion of its range there are several widely spreading species, and in the northern portion, the species are largely endemic to limited areas. It contains two sections including fourteen species. Their geographical distributions are as illustrated in Map 1.

Section 1. POECILOSTIGMA Koehne

Philadelphus subg. I. **Gemmatus** sect. 1. **Poecilostigma** Koehne in Gartenfl. **45**: 450. 1896; et in Mitt. Deutsche Dendr. Ges. **1904**(13): 77. 1904, pro parte.

Philadelphus sect. *Poecilostigma* Koehne. ll.cc. — Engler, Pflanzenf. ed. 2, **18a**: 191. 1930.

Philadelphus Mexicani Rydb. in N. Am. Fl. **22**: 164. 1905, in clavis, s. stat.

Philadelphus ser. *Gemmati* (Koehne) Rehder, Man. Cult. Trees Shrubs ed. 2, 275. 1940; et Bibliogr. Cult. Trees Shrubs 194. 1949, pro parte.

TYPE SPECIES: *P. mexicanus* Schlechtendal.

Arching shrubs or vines, the current year's growth pubescent and usually verrucose, the axillary buds exposed; leaves remotely denticulate or serrate, the base rounded, 3- or 5-nerved, the apex acuminate, rarely acute; inflorescences depauperate panicles, or flowers solitary, the bracts linear or lanceolate, foliaceous; hypanthia subglobose or cyathiform, the sepals foliaceous, (5–) 8–20 mm. long; corolla usually disciform, often pubescent; stamens 40–50; disc conic, style (3–) 4–7 mm. long, the stigma broadened and cristate; fruit obovoid-ellipsoid; seeds long-caudate. Seven species, Mexico to Panama.

KEY TO THE SPECIES

A. Flowers many on ramified branches; hypanthia subglobose.
  B. Inflorescences loose, paniculate, the secondary axis of unequal length, 4–30 mm. long, the lower ones longer.
    C. Hypanthia glabrous or with few weak pilose hairs; base of the hairs on the stem not thickened; axillary buds subglobose ..... 1. *P. affinis*.
    CC. Hypanthia pubescent; base of the hairs on the stem thickened; axillary buds conic.
      D. Hypanthia lanate, the underneath tissue obscure; inside of the petals glabrous ..... 2. *P. karwinskyanus*.
      DD. Hypanthia villose, the underneath tissue visible; petals pubescent on the apical ends ..... 3. *P. pueblanus*.
  BB. Inflorescences compact, raceme-like, the secondary axis equal in length, 2–4 mm. long, the flowers crowded at the end of elongated leafy branches ..... 4. *P. myrtoides*.

AA. Flowers solitary or ternate; hypanthia cyathiform or obconic (except *P. glabripetalus*).

B. Petals pubescent on both surfaces; hypanthia sparsely villose or pilose.

C. Style and disc pubescent; axillary buds conic; leaves large, 5–11 cm. long, the petioles 8–10 mm. long ..... 5. *P. mexicanus.*

CC. Style and disc glabrous; axillary buds subglobose; leaves small, 1–3.5 cm. long. the petioles 2–3 mm. long ..... 6. *P. austro-mexicanus.*

BB. Petals glabrous, at least on the inside; hypanthia lanate ..... 7. *P. glabripetalus.*

MAP 1. Geographical distribution of the species and sections of *Philadelphus* in the subgenus Gemmatus.

1. **Philadelphus affinis** Schlecht. in Linnaea 13: 419. 1839. — Walp. Rep. 2: 151. 1843. — Hemsl. in Biol. Centr. Am. 1: 383. 1879. — Koehne in Gartenfl. 45: 487. 1896; et in Mitt. Deutsch. Dendr. Ges. 1904(13): 78. 1904. — Schneider, Ill. Handb. Laubh. 1: 362. 1905. — Rydb. in N. Am. Fl. 22: 171. 1905. — Standl. in Contr. U. S. Nat. Herb. 23: 511. 1922. — Engler, Pflanzenf. ed. 2. 18a: 191. 1930.

Philadelphus zeyheri sensu Hemsl. in Biol. Centr. Am. 1: 384. 1880, non Schrader ex DC. 1828.

TYPE: Ehrenberg, Barranca de la Hacienda Del Carmen, S. Mexico.

An arching shrub or vine up to 4 meters high, the flowering branches slender, 10–20 cm. long, bearing 3 to 5 pairs of leaves, sparsely pilose, the base of the hairs not thickened; axillary buds subglobose, pubescent. Leaves ovate rarely ovate-elliptic, 4.5–8 cm. long, 2.5–4.5 cm. wide, rounded, rarely subcordate at the base, 5-nerved, acuminate at the apex, remotely serrate, each side with 2 to 5 teeth, subglobose or very sparsely strigose on both surfaces, more so on the principal nerves beneath, reticulations obscure above, conspicuous beneath, petioles 3–10 mm. long, pilose. Inflorescences depauperated panicles (Pl. V fig. 1) with 5-, rarely 3-, 1-, or 11-flowers, the woody part of the stalk 1–3 cm. long, pubescent as are the branchlets, bracts linear, the pedicels 2–3 mm. long, glabrous, after fruit up to 6 mm. long; hypanthia subglobose, 6 mm. in diameter, glabrous or with few weak pilose hairs, the sepals ovate, acuminate, 10 mm. long, 4–5 mm. wide, glabrous or very sparsely pilose; corolla subdisciform, 3.5–5 cm. across, the petals obovate to suborbicular, 1.3–1.8 cm. in diameter, glabrous, the apex round; stamens about 50, the longest three-fourths the length of the petals; disc subconic, glabrous; style 7 mm. long, undivided or the upper one-fifth separated, hirsute, the stigmas broadened, cristate, the abaxial surfaces broader and longer than the adaxial ones, the sterile portion hirsute (Pl. V fig. 1a). Capsules ellipsoid, the persistent calyx circumferential, the seeds long-tailed.

MEXICO: Hidalgo: Zacualtipán, *P. Maury 5826* (NY), same locality, *H. E. Moore 3238* (BH, G); in a barranca below Trinidad Iron Works, *C. G. Pringle 8833* (F, G, MO, NY, US); Atotonilco, *Schiede*, June 1830 (A, US); Bluff above Cuera Humada, *A. J. Sharp 4618* (TENN.). Tamaulipas: Tampico, Real del Monte, *M. Berlandier 333* (F, MO, US). Without precise locality, Herb. Dendrol. *Schneider* (A).

The type not being available, this interpretation is made on the basis of Schlechtendal's original description and Koehne's supplementary remarks. Schlechtendal characterized the inflorescences as 5-flowered racemes, the peduncles and calyces smooth and glabrous. Unfortunately he did not mention the pubescence of the style. For this character I rely upon Koehne who certainly had access to the now destroyed type. According to Koehne the style of this species has loose stiff hairs. I therefore place the Mexican material with 5-flowered depauperate panicles, more or less glabrous hypanthia and calyces, and pubescent styles with *P. affinis* Schlecht. Hemsley in 1880 doubtfully published *Berlandier 333* from Tampico as *P. zeyheri* Schrad. In this he mistook the material of a spontaneous Mexican species, *P. affinis* Schlecht., for a garden form cultivated in European gardens.

The ovate leaves, the subglobose glabrous hypanthia, the large foliaceous sepals with acuminate apices, the large number of stamens, the broadened stigmas and the ellipsoid capsules with circumferential persistent sepals of this species all suggest relationship to *P. inodorus* Linn. of the southern Appalachian region of the southeastern United States. As

the latter species has enclosed buds and this one has exposed buds their separation must have taken place far back in geological time.

In Mexico this species occurs on the Sierra Madre Oriental at altitudes of 1852–2000 meters, in regions where the annual rainfall attains at least 80 inches per year. Its white fragrant flowers appear from April to June. The specimens collected in July are with fruits.

2. **Philadelphus karwinskyanus** Koehne in Gartenfl. **45**: 486. 1896; et in Mitt. Deutsch. Dendr. Ges. **1904**(13): 1904. — Schneider, Ill. Handb. Laubh. 1: 362. 1905. — Rydb. in N. Am. Fl. **22**: 170. 1905. — Standley in Contr. U.S. Nat. Herb. **23**: 311. 1922.

Philadelphus scandens Moore in Bailey, Stand. Cycl. Hort. **5**: 2582. 1916.

TYPE: Karwinsky, Tolotapa, Oaxaca, Mexico.

A subscandent shrub up to 4 meters high, branchlets slender, the flowering ones over 50 cm. long, much ramified, terete, striate, villose, the base of the hairs thickened; axillary buds conic, villose. Leaves ovate, 4–7.5 cm. long, 2–3.5 cm. wide, rounded at the base, acuminate at the apex, 5-nerved, reticulations conspicuous beneath, remotely sharp serrate, 5–8 teeth on each side, sparsely strigose on both surfaces; petiole 5–10 mm. long, attached on cushion-like projections of the node. Inflorescences with 5 31 flowers, in a loose depauperate panicle, the woody portion below the pedicel 4–20 mm. long, pubescent, the pedicels 2–5 mm. long, thickly strigose and lanate; hypanthia subglobose, 4 mm. in diameter, strigose-lanate, the sepals ovate, 5–8 mm. long, densely lanate, the hairs entirely obscuring the tissue beneath; corolla 2.5–3 cm. across, the petals obovate-suborbicular 0.8 13 mm. in diameter, sparsely pubescent along the median dorsal line, glabrous on the ventral side, the apex rounded; stamens about 45, the longest half as long as the petals; disc subconic, pubescent, stigmas 2.5–3 mm. long, enlarged cristate, the sterile portion pubescent, the abaxial surface with 2 papillose ridges. Capsule and seed not known.

MEXICO: Oaxaca: Tepascolula, *Loesener 1421*(G); Huitzo, *L. C. Smith 807*(G). Vera Cruz: Orizaba, *F. Müller*, Jan. 1853(NY). Sinaloa: Mazatlan, *J. G. Ortega 6770*(F). Without precise locality, *Ortega 7342*(F).

UNITED STATES: Cultivated in California: Altadena, *F. W. Peirson 79*(BH); San Diego, *F. G. Woodcock 870*(F), *871*(BH), *872*(A, BH); Santa Monica, *L. H. & Ethel Bailey 7804*(BH); Los Angeles, *L. H. & Ethel Bailey 9117*(BH).

A great altitudinal variation is reported for this species. In Oaxaca it has been collected 2000 meters above the sea level and in Sinaloa, it has been reported from humid lowlands almost at sea level. It is an evergreen shrub, flowering all year around. In California where it is an introduced and cultivated species, flowering records cover August, October, December, January, February, March, April and May.

3. **Philadelphus pueblanus,** sp. nov.

Frutex subscandens, usque 4 m. altus, ramulis floriferis, 20–40 cm. longis, teretibus, striatis, 2–4 mm. diametro, dense pilosis et sparse strigosis, pilis basi incrassatis, gemmis axillaribus breviter, villosis; foliis ovatis, 4–7 cm. longis, 2–3.5 cm. latis, basi rotundatis, raro obtusis, quintuplinerviis, apice acuminatis, serratis vel subintegris, dentibus utrinque 1, 2 usque ad 5, utrinque strigosis, petiolo 5–10 mm. longo; inflorescentiis ramosis, 5- usque 31-floribus, pedunculis 4–20 mm. longis, pedicellis 3–6 mm. longis, villosis, verruculosis, hypanthiis subglobosis, 4 mm. diametro, villosis; sepalis ovatis, caudatis, 10 mm. longis, 4–5 mm. latis, sparse villosis; corolla disciformii, 4 cm. diametro, petalis oblongo-suborbiculatis, 2 cm. longis, 1.5 cm. latis, partibus medianis extus hirsutis, apice rotundatis et retusis; staminibus ca. 40; disco subconico, medio hirsuto; stylis 6–7 mm. longis, columnaribus indivisis; pubescentibus; stigmatibus cristatis, 2–3 mm. longis, partibus sterilibus hirsutis; capsulis et seminibus ignotis.

MEXICO: Puebla: vicinity of Puebla, *Bro. G. Arsène* (*Bro. Nicolas*) *171* (A, TYPE; G, MO, NY, US ISOTYPES); Arzobispado, *Bro. G. Arsène 10136*(US); Ixtaccihuatl, *C. A. Purpus 169*(MO, US); Com. Geogr.-Expl. Rep. Mexicana *1022*(NY). Tlaxcala: Tlaxcala, *E. K. Balls 4906*(A). San Luis Potosi: Santa Barbara, *Bro. G. Arsène 10093* (US). Mexico: Par Nicolas, *M. Bourgeau 995*(US); Temascaltepec, Rincón, *G. B. Hinton 2362*(A), *5032*(BH, NY, US). Michoacan: Zitacuaro, *G. B. Hinton 13342*(G, NY, US). Morelos: near Cuernavaca, *J. N. Rose & W. Hough 4412*(US).

This species is intermediate between *P. affinis* Schlecht. which has glabrous or subglabrous hypanthium and *P. karwinskyanus* Koehne in which the hypanthium is thickly lanate with the indumentum entirely covering the epidermal tissue. In Puebla it occurs at altitudes between 1700 and 2194 meters as semiscandent shrubs in thickets and among trees in ravines. Its pale yellow sweet-scented flowers appear from March to October.

4. **Philadelphus myrtoides** Bertol. Fl. Guatim. 21. pl. 7. 1840. — Walp. Rep. **2**: 151. 1843. — Hemsl. Biol. Centr. Am. **1**: 383. 1879. — Koehne in Gartenfl. **45**: 487. 1896. — Rydb. in N. Am. Fl. **22**: 170. 1905. — Engler, Pflanzenf. ed. 2, **18a**: 192. 1930. — Standley in Field Mus. Nat. Hist. Bot. Ser. **18**: 474 (Fl. Costa Rica). 1937.

Philadelphus trichopetalus Körnicke in Gartenfl. **16**: 73. 1867. — Koehne in Gartenfl. **45**: 487. 1869; et in Mitt. Deutsch. Dendr. Ges. **1904**(13): 78. 1904. — Smith in Pittier, Prim. Fl. Cost. II. **1**: 90. 1898. — Schneider, Ill. Handb. Laubh. **1**: 364. 1905. — Engler, Pflanzenfam. ed. 2, **18a**: 192. 1930.

Philadelphus mexicanus sensu Moore in Bailey, Stand. Cycl. Hort. **5**: 2582. 1916, pro parte. — Standley & Calderón, Pl. Salv. 88. 1925, non Schlechtendal.

Philadelphus sempervirens Hort. ex. Moore in Bailey, Stand. Cycl. Hort. **5:** 2582. 1916.

Philadelphus matudai Lundell in Contr. Univ. Mich. Herb. **4:** 6. 1940.

TYPE: Botanical Garden of Bologna, Italy.

An arching shrub, 2–4 m. high, flowering branches slender, 21–50 cm. long, with 14 or more pairs of leaves, longitudinally striate, rather densely villose, the trichomes slightly curled, their base more or less thickened; buds small, rounded, densely brown villose. Leaves ovate, 3–4 cm., rarely up to 5.5 cm. long, 1–2.8 cm. wide, sparsely strigose above, more so beneath, the hairs glandular at the base, rounded or rarely obtuse at the base, acuminate at the apex, subentire, or remotely denticulate, with 2 to 6 sharp teeth projecting outward on each side, triplinervate or quintuplinervate, reticulations obscure on both surfaces; petioles 6–9 mm. long, strigose. Flowers 5, rarely 1, 3, or 7, crowned at the end of long slender branchlets, the woody portions below the pedicels uniformly short, 2–4 mm. long, the bracts linear, 5–13 mm. long, the pedicels 3–4 mm. long, white lanate; hypanthia subglobose, 5 mm. in diameter, densely lanate; sepals ovate, acuminate, 8 mm. long, 4 mm. wide, lanate; corolla disciform, 3–4 cm. in diameter, the petals suborbicular-ovate, 1.2–1.8 cm. long, 1.1–1.7 cm. wide, slightly hirsute along the median longitudinal line on both surfaces, the apex rounded; stamens ca. 44, the longest half as long as the petals; disc subconic, pubescent, the style 3–4 mm. long, pubescent, the stigmas 3 mm. long, enlarged, cristate, the abaxial surface as long as the adaxial, the sterile portions hirsute; capsules and seeds not known.

MEXICO: Chiapas: Volcano Tacana, *E. Matuda 2791* (ISOTYPE of *P. matudai* Lundell, A, F, G, NY, US).

GUATEMALA: Alta Vera Paz: Vicinity of Cobán, *P. C. Standley 92452*(F). Guatemala: near Finca La Aurora, *Ignacio Aguilar 82*(F). Huehuetenango: near Chiantla, *P. C. Standley 82517*(F). Sacatepéquez: near Antigua, *P. C. Standley 60316*(F); *S. Hayes* (G). Quezaltenango: *P. C. Standley 86561*(F, US). Suchitepéquez: vicinity of Finca Alvidas, *J. A. Steyermark 35458*(F).

EL SALVADOR: San Salvador: *S. Calderón 687* (F, G, US, MO, NY); *M. C. Carlson 435*(F). Ahuachapán: near Ataco, *P. C. Standley & V. E. Padilla 2726*(F).

HONDURAS: Morazan: Tegucigalpa, *J. V. Rodriguez 3173*(F).

COSTA RICA: Cartago, Cervantes, *A. Tonduz 10444*(US); San José, *Tonduz 1492*(US); Las Cóncavas, *P. C. Standley 36006*(US); Tapisca de Zaruro, *Austin Smith 185*(US).

PANAMA: Chiriqui: vicinity of Bajo Mona and Quebrada Chiquero, *R. E. Woodson & R. W. Schery 588*(MO).

CULTIVATED: California: Santa Barbara, *E. P. Bradbury*, Oct. 10, 1915(BH).

The identification of this species is based on Bertoloni's description and illustration. In his illustration he characterized *P. myrtoides* as a plant

with rather small ovate-elliptic leaves on the flowering branches which terminate with crowded cluster of several flowers each in the axil of a reduced leaf. Among the available collections of Guatemalan *Philadelphus*, Bertoloni's description and illustration conforms in all respects to *Standley 60316, 82417* and *Steyermark 35458*. It is also well represented by *Calderón 687* from El Salvador. *Matuda 2791* represents the northern limit of the range of the species. Bradbury's collection from Santa Barbara, in Bailey Hortorium, was identified as *P. sempervirens* Hort. This specimen was probably Moore's material basis for the publication of his *P. sempervirens*.

Although 110 years have elapsed since *P. myrtoides* was published, it has not been well understood. Körnicke was probably not aware of Bertoloni's species when he published *P. trichopetalus* from Costa Rica. According to his description the Costa Rica plant has flowers clustered at the end of a branchlet, and the petals of the flowers are softly pilose. I have not seen Körnicke's type. But judging from the Costa Rica and Panama collections I have examined and by our present knowledge of the distribution of the various species of *Philadelphus* in Central America, *P. trichopetalus* Körnicke and *P. myrtoides* Bertol. are conspecific.

Philadelphus myrtoides is the most southern species of the genus. It has been collected on the high mountains from Chiapas in Mexico through Guatemala, El Salvador, Honduras south to Costa Rica and Panama. In Guatemala it occurs in cypress groves at altitudes ranging from 1200 to 1930 meters. Standley suggested the possibility of it being introduced and cultivated in Costa Rica. Some of the El Salvador collections were from gardens. Apparently this species has been widely cultivated in Central America where it flowers from January to August. The creamy white fragrant flowers are sold in the markets for decorative purposes under the name "Mosqueta."

Philadelphus myrtoides is closely related to *P. karwinskyanus* Koehne but the latter species can be distinguished for its elongated peduncles and its petals being glabrous on the inner surface.

5. **Philadelphus mexicanus** Schlecht. in Linnaea 13: 418. 1839. — Walp. Rep. 2: 151. 1843. — Hemsley in Biol. Centr. Am. 1: 384. 1879, excl. spec. Seemann, Coulter, Ghiesbreght. — W. G. Smith in Gard. Chron. n.s. 19: 753, fig. 123. 1883. — Burbidge in Gard. Chron. III. 34: 218, fig. 89. 1903. — Hook. f. in Bot. Mag. 124: pl. 7600. 1898. — Koehne in Gartenfl. 45: 487. 1896; et in Mitt. Deutsch. Ges. 1904(13): 78. 1904. — Wittmack in Berl. Gartenz. 1883: 528. fig. 91. 1883. — Dippel, Handb. Laubh. 3: 335. 1893. — Schneider, Ill. Handb. Laubh. 1: 362, fig. 234 b–b.^{2} 1905. — Rydb. in N. Am. Fl. 22: 170. 1905. — Standley in Contr. U. S. Nat. Herb. 23: 311. 1922. — Rehder, Man. Cult. Trees Shrubs 280. 1927, ed. 2, 275. 1940; et Bibliogr. Cult. Trees Shrubs 195. 1929. — Hansell. Mexico Pl. 162. 1935. — Bean, Trees Shrubs ed. 7, 2: 419. 1950; et in Chitt. Dict. Gard. 3: 1546. 1951.

A scandent evergreen shrub to 5 meters high with long drooping branches, the second year's growth 3–4 mm. in diameter, castaneous, rugose, the bark closed, longitudinally rimulose, the current year's growth 1.5–2 mm. in diameter, hirsute, the trichomes with more or less thickened bases; axillary buds conic, the first few below the flowers often developing into virgin shoots. Leaves ovate, 5–11.5 cm. long, 2–5 cm. wide, very sparsely strigose on both surfaces, rounded or obtuse or subcordate at the base, 5- or rarely 3-nerved, acuminate at the apex, subentire or with 1 to 6 tooth-like projections on each side, reticulations obscure above, conspicuous beneath, the petioles 8–10 mm. long, strigose. Flowers solitary, yellowish white, very fragrant; pedicels hirsute, 1–3 mm. long, bracts lanceolate, 1–2 cm. long; hypanthia cyathiform, sparsely villose, the trichomes slightly curly; sepals foliaceous, ovate, long acuminate or cordate, 10–20 mm. long, 7 mm. wide, sparsely villose, the hairs tending to curl slightly; corolla 3–4 cm. across, the petals suborbicular, hirtellous on both surfaces; stamens ca. 40, the anthers oblong; disc subconic, hirsute at the center, the styles 3 mm. long, pubescent, the upper half divided, the stigmas 3 mm. long, cristate, the abaxial surface much longer than the adaxial one, the sterile portion often hairy. Capsules obovoid-ellipsoid, the lower portion near the base quadrangular, about 12 mm. long, 10 mm. in diameter, the persistent calyx subcircumferential. Seeds long-caudate.

MEXICO: Mexico: Amecameca, *G. L. Fisher* on July 29, 1924(F, MO, US); Federal District, *A. J. Sharp 445* (A,TENN); Mts. of Toluca, Halstead (NY). Guerrero: Omiltemé, *A. J. Sharp 441551* (A, TENN). Michoacán: Morelia, Cerro Azul, *Bro. G. Arsène 5141* (F,G,MO,US). Oaxaca: Cerro de San Felipe, *C. Conzatti & V. Gonzalez 471*(G); *H. Galeotti 2850*(US); *E. W. Nelson 1398*(G,US). Chiapas: Siltepec, *E. Matuda 1701*(A,MO,US). Vera Cruz: Jalapa, *S. Schiede*(G,NY, ISOTYPES); Orizaba, *Botteri 1105*(G, US). Puebla: Cero Guadelupe, *Nicolas*, June 10, 1909(F).

GUATEMALA: Huehuetenango: San Juan Ixcoy, *A. J. Sharp 4616*(F); definite locality not given, *J. D. Smith*, April 9, 1896(G); Cerro Cananá, Sierra de los Cuchuatanes, *J. A. Steyermark 49059*(F); Aguacatàn, *P. C. Standley 91218*(F). Quezaltenango: Volcán de Santa Maria, *P. C. Standley 83535*(F); *J. A. Steyermark 33985*(F); Palestina, *P. C. Standley 84230*(F); Santa Maria de Jesús, *P. C. Standley 84860*(F); above Mujuliá, *P. C. Standley 85608*(F, US); Zunil, *P. C. Standley 85647*(F); Volcán Santo Tomas, *J. A. Steyermark 34952*(F). Quiché: *O. F. Cook 31*(US); San Miquel Uspantán, *Heyde & Lux* (distributed by *J. D. Smith*) *3046*(G, NY, US); Chajul, *A. J. Sharp 4681*(F). Sacatepequez: Volcán de Auga, *P. C. Standley 65124*(F). Chimaltenango: Santa Elena, *D. S. Johnson*, Aug. 10, 1932(F); *A. F. Skutch 335* (A, US). Sololá: Volcán San Pedro, *J. A. Steyermark 47253*(F, US); Volcán Atitlán, *J. A. Steyermark 47527*(F). San Marcos: Volcán Tajumulco, *J. A. Steyermark 35661*(F). Without precise locality, *F. C. Lehmann*, June 1882(US).

CULTIVATED: California: Berkeley, in the garden of A. Blake, *N. F. Bracelin, 1354*(BH).

As the natives of Mexico had cultivated species of *Philadelphus* from early times it is inevitable that certain garden forms had been produced by them. It happened that the first published Mexican species was based on a double flowered form. Schlechtendal cited three specimens, Schiede from Jalapa, Mühlenpfordt from Oaxaca and a specimen from Mexico in Herb. Lehmann. Of these I have seen only the duplicates of Schiede's collection, which agree with Schlechtendal's description. Thus the double flowered form typifies the species. Apparently this form is found only or chiefly in the states of Vera Cruz and Puebla where the mean annual temperature is between 62–67° F. and the mean annual rainfall is 40–80 inches. The Bracelin collection is the only specimen from a cultivated plant outside of Mexico that I have seen. It has been reported that the cultivated plants climb to 12 meters and their flowers are yellowish or deep cream white.

Specimens collected from the wild population all have simple flowers. Compared with the isotypes of typical *P. mexicanus* Schlecht., I can detect no other characters from the above cited specimens to distinguish them as a form besides their possession of the simple flowers. Like the double-flowered form, their petals are pubescent on both surfaces, the disc and style are pubescent, and the hypanthium is sparsely villose with the trichomes slightly curled. In general, their leaves are larger and more prominently quintuplinervate than the double flowered form. But this 5-nerved condition is also true with the large leaves of the cultivated specimens. It seems that with both the wild and the cultivated material, at the base of each leaf, there is a pair of small nerves originated from the petiole and running along the basal portion of the margin. When the leaves are small, these nerves are so closely pressed against the margin that they appear inconspicuous.

In Mexico this species occurs at altitudes of 2280–3000 meters in Oaxaca. In Huehuetenango, it has been recorded at altitudes of 1950–3160 meters on steep limestone slopes of damp oak forests. In Quezaltenango it occurs at altitudes of 1500–3000 meters in sunny thickets, damp sandy hillside forests or in wet brushy ravines as subscandent shrubs. In Sololá it occurs in damp cloud forests.

The vernacular names reported are "Mosqueta" and "Azahar," the former more widely applied. Hernandez (1651) in "Nova Plantarum Mexicanorum Historia" discussed and illustrated a plant with opposite leaves and a cluster of two simple flowers under the name, *Acuilotl* or Volubili Aquatica. He mentioned it as growing in wet places, creeping on the ground or scrambling up trees. This record has been regarded by Schlechtendal, Lindley, Hooker and many modern authors as representing *P. mexicanus* Schlecht. To the Mexican Indians this species is economically rather important. They employ the flowers both in preparing perfume and for making garlands. The leaves are taken in wine for the relief of colic, or crushed and applied as a plaster to ease strained members and dissolve tumors.

The pubescent petals and simple flowers of this species resemble those

of the flowers of *P. myrtoides* Bertol. But the latter species can be readily distinguished by its clustered flowers and densely lanate hypanthium.

6. **Philadelphus austro-mexicanus,** sp. nov.

Philadelphus mexicanus sensu Decaisne in Rev. Hort. III. 1: 381, fig. 20. 1852. non Schlechtendal. 1839.

Frutex ramosissimus, ramulis floriferis brevibus, ca. 3 cm. longis. 1 mm. diametro, castaneis, rugoso-strigosis, pilis basi incrassatis, gemmis axillaribus subglobosis, pilosis; foliis ovatis vel ovato-lanceolatis, 1 3.5 cm. longis, 0.5–1.5 cm. latis, basi subrotundatis, triplinerviis, apice subacuminatis vel acutis, serratis, utrinque 1- usque 5-serratis utrinque sparse strigosis vel praeter nerviis subglabris, petiolo 2 3 mm. longo; floribus solitariis, pedicellis 2 mm. longis, strigosis; hypanthiis obconicis, 3 mm. longis, 4 mm. diametro, sparse pilosis; sepalis ovatis, 9–11 mm. longis, caudatis, sparse pilosis vel subglabris; corolla disciformi, 3.8–4 cm. diametro, petalis obovatis, 1.5–1.7 mm. longis, 1.3 mm. latis, utrinque in partibus medius hirsutis; staminibus ca. 52, disco glabro, stylis 4 mm. longis, glabris, partibus superioribus liberis, stigmatibus dilatatis, cristatis; capsulis et seminibus ignotis.

MEXICO: Chiapas: *Dr. Ghiesbreght 813* (G, TYPE; F, MO, ISOTYPES; A, fragment of ISOTYPE).

The rugose branchlets, the dentation of the leaves, the large sepals, the pubescent petals, the numerous stamens, the divided style and the dilate-cristate stigmas of this species all suggest a close relationship to *P. mexicanus* Schlecht. But it can be readily distinguished by its small leaves, very sparsely pilose hypanthium and sepals and its glabrous styles.

Decaisne's figure represents a plant with small leaves. His concept of Schlechtendal's species was apparently based on a Ghiesbreght collection, very likely a part of the same collection of which three specimens are available to me. All of them have small leaves and glabrous styles.

7. **Philadelphus glabripetalus,** sp. nov.

Philadelphus mexicanus sensu Lindl. Bot. Reg. 26(Misc.): 37. 1840; et 28: pl. 38. 1842. — sensu Hemsl. in Biol. Centr. Am. 1: 384. 1879, pro parte, non Schlechtendal, 1839.

Frutex ramosissimus, ramulis floriferis 5–15 cm. longis, 1–1.5 mm. diametro, rugoso-hirsutis, pilis basi incrassatis; foliis ovatis vel ovato-lanceolatis, 1.5–6 cm. longis, 1–2.5 cm. latis, basi rotundatis, triplinerviis, apice acuminatis, subintegris vel serratis, dentibus utrinque 1 vel 2, raro 4, supra subglabris vel sparse villosis, subtus sparse villosis; petiolo 3–5 mm. longo, villoso; floribus solitariis vel raro ternatis, pedicellis 3–5 mm. longis, dense villosis, hypanthiis subglobosis, 5 mm. diametro, lanatis; sepalis ovatis, 10–15 mm. longis, 5 mm. latis, acuminatis; corolla 2.5–3 cm. diametro, petalis obovatis, vel suborbicularibus, 1–1.3 cm. longis, 9–10 mm. latis, utrinque glabris, vel extus hirsutis, staminibus ca. 60;

disco medio hirsuto, stylis glabris vel basi hirsutis, 3–4 mm. longis, stigmatibus cristatis, 4 mm. longis, supra liberis; capsulis et seminibus ignotis.

MEXICO: Federal District: Sierra de Ajusco, *C. G. Pringle 6311*(A, TYPE; G, MO, NY, US, ISOTYPES). Puebla: Moria, *Nicolas*, in February 1908(F). Without precise locality, *P. Maury 3158*(NY), *3822*(NY).

The shape of the leaves, the solitary flowers and the glabrous petals suggest a relationship to *P. osmanthus* S. Y. Hu, but the latter species has strigose lower leaf-surfaces and hypanthia, and short styles while the present species has villose lower leaf-surfaces, lanate hypanthium, and styles 3–4 mm. long. It differs from *P. mexicanus* Schlecht. in having glabrous petals and smaller leaves. Its solitary or ternate flowers also suggest relationship with *P. coulteri* S. Wats. but the latter species has densely villose hypanthia with the epidermis entirely obscured. In the Federal District, this species occurs at altitudes 2400–2470 meters. It climbs among shrubs up to 5–7 meters high. Specimens collected from June to September all bear flowers. This suggests that like many other Mexican *Philadelphus*, this species has a very long flowering period; of course, local climatic conditions may be involved.

Judging by the figures and the descriptions given by Lindley (1842), his material which was introduced by Hartweg from the Hacienda del Carmen, could not be the true *P. mexicanus* Schlecht. for it has small leaves and a glabrous style while Schlechtendal's species has large leaves and a pubescent style. As Lindley described the hypanthium and calyx of his material as densely pubescent, this eliminates the possibility of it being *P. austro-mexicanus* S. Y. Hu which is another small-leaved Mexican species, for the latter has more or less glabrous hypanthium and calyx, and pubescent style. By the process of elimination, one may logically come to the conclusion that the material Hartweg introduced to the European gardens belongs here.

Section 2. **Coulterianus**, sect. nov.

Philadelphus subg. I. **Gemmatus** sect. **Coulterianus**, sect. nov.

TYPE SPECIES: *P. coulteri* Wats.

Frutex erectus vel subscandens, ramulosis hornotinis pubescentibus, plerumque verrucosis, gemmis axillaribus expositis; foliis integris, raro denticulatis vel inconspicue serratis, basi rotundatis vel obtusis, raro acutis, triplinerviis; apice acutis vel obtusis; floribus solitariis vel raro ternatis; hypanthiis subglobosis, pubescentibus; sepalis ovatis, 3–8 mm. longis, corolla cruciformi vel disciformi; staminibus 30 usque ad 44; disco plano, stylo 1–3 mm. raro 4 mm. longo, stigmatibus noncristatis; capsulis subglobosis; seminibus longo-caudatis.

Seven species, all in northeastern Mexico.

KEY TO THE SPECIES

A. Lower leaf-surface pilose or strigose; stems rugosely hirsute, the base of the trichomes thickened.

B. Hypanthia pilose, the epidermal tissue visible; the lower leaf-surface pilose ..... 8. *P. osmanthus.*
BB. Hypanthia densely villose, the epidermal tissue obscure; the lower leaf-surface strigose.
C. Leaves oblong; pedicels 5–8 mm. long; petals emarginate at the apex ..... 9. *P. oblongifolius.*
CC. Leaves ovate; pedicels 2–3 mm. long; petals rounded at the apex.
D. Style and center of disc pubescent; leaves on flowering shoots 2–3 cm. long ..... 10. *P. coulteri.*
DD. Style and center of disc glabrous; leaves on flowering shoots 1–2 cm. long. ..... 11. *P. asperifolius.*
AA. Lower leaf-surface densely villose; stem pilose, the base of the trichomes not thickened.
B. Leaves subcoriaceous, hispid above, densely villose and appearing white beneath.
C. Style pubescent ..... 12. *P. sargentianus.*
CC. Style glabrous ..... 13. *P. pringlei.*
BB. Leaves characeous, weakly pilose above, very sparsely villose beneath; style glabrous ..... 14. *P. calcicolus.*

8. **Philadelphus osmanthus,** sp. nov.

Frutex subscandens, 1.3 m. altus, ramosissimus; ramis robustis, 3–5 mm. diametro, fumeis, longitudinaliter rimulosis, bienniis 2 mm. crassis, castaneis, striatis, rugoso-hirsutis, corticibus clausis, hornotinis 1–1.5 mm. diametro, pilis basi incrassatis, gemmis conicis, strigosis, pilis luteis; foliis ovatis, raro ovato-lanceolatis, 2–6 cm. longis, 0.8 cm. latis, basi obtusis, apice acutis vel obtusis, apiculatis, integris vel utrinque 1 vel 3 serrulatis, utrinque strigosis, pilis eburneis, petiolo 4–9 mm. longo; floribus 1, raro 3, terminalibus, bracteis linearibus, 3–10 mm. longis, pedicellis 5–10 mm. longis, cum hypanthiis et calycibus incano-pilosis, hypanthiis subglobosis, 5–7 mm. diametro; sepalis ovatis, acuminatis, 7–8 mm. longis; corolla subcruciformi, 2.5–3.2 cm. diametro, petalis obovatis, apice emarginatis, 1.2–1.5 cm. longis, 0.7–1.2 cm. latis; staminibus ca. 36; disco medio piloso, stylo brevissimo, 1 mm. longo, vix hirtello, stigmatibus 3 mm. longis, cristatis, supra divisis; capsulis ellipsoideis vel subglobosis, 6–8 mm. diametro, calycibus persistentibus supra medium affixis; seminibus longocaudatis.

MEXICO: Hidalgo: Jacala, *V. H. Chase 7310* (NY, TYPE; A, F, G, MO, ISOTYPES).

This species occurs in woods in deep ravines at an altitude of 1525 meters. Unlike other species of the genus, the lateral buds on the branchlets of this one are suppressed from normal development. Thus its flowering shoots are largely developed from the terminal buds, a very unusual character in *Philadelphus*. The thickened base of the epidermal hairs on the branchlets, the elongate stigmas and the pubescent disc of this species suggest relationship to *P. coulteri* Wats. The latter species can be dis-

tinguished by the thickly villose hypanthium. The subentire leaves sparsely strigose and the long-tailed seeds of this species also suggest a remote relationship with the southern Appalachian species *P. inodorus* Linn. which has enclosed axillary buds. The very short style conforms to Körnicke's description of *P. asperifolius*, a species with glabrous style and disc.

9. **Philadelphus oblongifolius,** sp. nov.

Frutex ramosissimus, ramis cinereis, ramulis gracilibus, bienniis 1–1.5 mm. crassis, brunneis, verrucoso-hirsutis, hornotinis 1 mm. diametro, pilis basi incrassatis; foliis oblongis, raro oblongo-ovatis, 1.3–2.5 cm. longis, 4–8 mm. latis, utrinque obtusis, apice apiculatis, margine integerrimis, utrinque strigosis, pilis subtus longioribus et densioribus, petiolo 3 mm. longo; floribus solitariis, pedicellis 6–8 mm. longis, incanis, hypanthiis calycibusque incanis; sepalis ovatis, 6 mm. longis, 2.5–3 mm. latis; corolla cruciformi, 3.5 cm. diametro, petalis obovatis, apice emarginatis, 1.6 cm. longis, 1.1–1.4 cm. latis; staminibus ca. 30; disco praeter medio glabro, stylo 5 mm. longo, supra diviso, basi dense hirsuto, stigmatibus 2 mm. longis. Capsulis ignotis.

MEXICO: San Luis Potosi: Minas de San Rafael, *C. A. Purpus 5368b* (A, fragment of TYPE; F, TYPE; MO, NY, ISOTYPES).

Through its strigose trichomes on the leaves, and pubescent styles this species is closely related to *P. Coulteri* Wats. It can be distinguished from *P. coulteri* by its slender branchlets, oblong leaves, long pedicellate flowers with emarginate petals and 5 mm. long styles.

10. **Philadelphus coulteri** Wats. in Proc. Am. Acad. 22: 472. 1887.

Philadelphus purpusii Brandegee in Univ. Calif. Publ. Bot. 4: 270. 1912.

TYPE: *Dr. Coulter 77*, Zimapan, Mexico (Gray Herbarium).

A subscandent shrub, the branches ferrugineous, the second year's growth 2–3 mm. in diameter, the bark rugose, closed, slightly longitudinally rimulose; the current year's growth rugose and hirsute, the trichomes with thickened bases. Leaves ovate, or ovate-elliptic, subentire, obtuse or acute, apiculate, rounded or rarely obtuse at the base, strigose on both surfaces, more so beneath, those on the flowering branches, 1.5–3 cm. long, 1–1.5 cm. wide, the petioles 3–4 mm. long. Flowers solitary, rarely ternate, the pedicels 2–3 mm. long, thickly villose and white like the hypanthia and calyx, the sepals ovate, 5–6 mm. long; corolla disciform, 2.5–3 cm. across, the petals orbicular-obovate, rounded at the apex; stamens 34–38; disc pubescent at the center, the style 2–3 mm. long, the upper half divided, the stigmas 2–2.5 mm. long, the abaxial surface pappilose, 2 mm. long, the adaxial surface half as long. Capsules and seed not known.

MEXICO: Hidalgo: Zimapan, *Dr. Coulter 77*(G, TYPE); woods above Minas Viejas between Zimapan and Jacala, *H. E. Moore, Jr. 2767*(G, BH); Atotonilco, *Schiede*, June 1830(NY). San Luis Potosi: Minas de San Rafael, *C. A. Purpus 4910*(MO), *5368*(F, G, MO, US ISOTYPES of *P. purpusii* Brandegee; A, photo and fragment). Tamaulipas: near Frank Harrison's "Rancho del Ciel" in Sierra de Guatemala above Gomez Tarias, *Sharp, Shank, Wolfe & Hernandez 52201* (A, TENN), *52060* (A, TENN).

Philadelphus coulteri Wats. was essentially based on *Coulter 77* collected from Zimapan. In publishing the species Watson also cited C. S. Sargent's collection from Monterey. As the species was named after Coulter, his number 77 in the Gray Herbarium should be the actual type of the species. Sargent's material is specifically distinct. It differs from the type of *P. coulteri* in having smooth pilose branchlets, leaves hispid above and densely long villose beneath and a very short style. In 1888 Watson published an illustrated account of *P. coulteri*. As Coulter's collection is rather fragmentary, that illustration was unfortunately drawn from Sargent's material. This publication has an out-reaching misleading effect in the identification of the true *P. coulteri* among botanists as well as horticulturists and consequently cytogeneticists.

Philadelphus coulteri Wats. was first collected in Zimapan. Additional material extends its range northward to Gomez in the State of Tamaulipas. At this area, the southeastern end of the Mexican Central Plateau, the plant grows, according to Moore, as a shrub a little over a meter high and its flowers are white, and fragrant. The standard reference books on cultivated shrubs have recorded this species as having purple-centered flowers. This is apparently incorrect.

Watson published this species in 1887 on the basis of a herbarium specimen. He did not know the flower color, nor did he indicate it in the description. The next year an illustrated account was published in Garden and Forest. Here no flower color was mentioned either. Three years later, Burbidge wrote Hemsley from Dublin, Ireland, saying, "Can you kindly give me the name of the enclosed? I cannot find it in the books. It exists in one or two old gardens here, where it is called Rose Syringa. Its sweet fragrance and purple-centered flowers are remarkable." What Hemsley reported we do not know, but this was later referred to *P. coulteri*. Meanwhile, Nicholson in the Supplement to the Garden Dictionary incorporated Watson's review of *P. coulteri* from the Garden and Forest. At the end of his summary Nicholson put down 1888, the year when his source material was published, as the year of the introduction of the plant into cultivation. Burbidge got this reference and in 1903 he published a note saying "There is a variety of *P. mexicanus* called *P. M. Coulteri*, introduced, it is said in Nicholson's Supplement, as recently as 1888; but probably this is a mistake as the shrub has existed for many years in old Irish gardens, where it is known as the "Rose Syringa" . . . and it differs from all other species or varieties . . . each of its four white petals has a purplish blotch at its base." This is a misinterpretation of Watson's figure and description and also a misidentifica-

tion of the Irish "Rose Syringa." But since that time in all major works on cultivated shrubs and even in books dealing principally with the flora of Mexico, the error in the flower color of *P. coulteri* Wats. has been perpetuated.

Claims have been made by hybridizers and cytogeneticists that *P. coulteri* Wats. is a grandparent of the triploid garden hybrids, "Belle Etoile," "Sybille" and "bicolor" which are segregates of *P. purpureo-maculatis* Lemoine.[1] There seems to be no record that true *P. coulteri* has ever been introduced into cultivation, thus it is impossible for it to have been a parent of *P. purpureo-maculatus* Lemoine. The above mentioned claims do not seem to have any material support. The Monterey region is better known botanically than Zimapan, the type locality of *P. coulteri.* Consequently the *Philadelphus* that Sargent collected is much better represented in American herbaria than is true *P. coulteri.* It was almost inevitable that these specimens should have been mistaken for *P. coulteri.* When typical *P. coulteri* Wats. was again collected by Purpus in 1911. Brandegee was misled into creating a new binomial, for *P. purpusii* Brandegee is the genuine *P. coulteri* Wats. *Purpus 5368*, the type number of *P. purpusii* Brandegee represents an aggregate of three elements, probably three separate collections combined under one number of which I have examined five sheets. The element with glabrous disc and style belongs to *P. asperifolius* Körnicke. The two other elements both have a pubescent disc and style. One of them has ovate leaves and styles shorter than the stigmas. This one agrees with Brandegee's description of *P. purpusii*, and is identical with the type of *P. coulteri* Wats. The other element has small oblong leaves and elongated style which is longer than the stigmas. It becomes the type of *P. oblongifolia* S. Y. Hu.

11. **Philadelphus asperifolius** Körnicke in Gartenfl. **16**: 73. 1867. — Koehne in Gartenfl. **45**: 487. 1896; et in Mitt. Deutsche. Dendr. Ges. **1904**(13): 78. 1904. — Schneider, Ill. Handb. Laubh. **1**: 364. 1905. — Rydb. in N. Am. Fl. **22**: 171. 1905. — Standl. in Contr. U.S. Nat. Herb. **23**: 310. 1922.

TYPE: *Karwinsky* July 1842, Hacienda Santyaguillo, Mexico (Herb. Hort. Petropol.).

An elegant shrub, 2–3 meters high, branchlets rigidly hirsute, the second year's growth gray, longitudinally rimulose, the bark closed, the current year's growth brown, pubescent, the hairs with thickened bases. Leaves ovate, those on the vegetative shoots up to 3 cm. long, 1.3 cm. wide, those on the flowering shoots 1.3–1.7 cm. long, 0.5 cm. wide, rounded at the base, obtuse and apiculate or subacute at the apex, both surfaces sparsely covered with rigid, straight appressed white hairs, the petioles 1–2 mm. long. Flowers solitary, subsessile, the pedicels 1–3 mm. long, canescent as are the hypanthia and the calyx, the sepals ovate, 3 mm. long; corolla disciform, 1.5–2 cm. across, the petals obovate, rounded at

[1] E. K. JANAKI AMMAL in Jour. Roy. Hort. Soc. **76**: 272. 1951.

the apex, twice the length of the sepals; stamens 30–38; disc glabrous, the style short, about 1.5 mm. long, undivided, glabrous, the stigmas separated, 2 mm. long, the abaxial surface twice as broad and as long as the adaxial one. Capsules subglobose, 6–7 mm. long, 7 mm. diameter, the persistent calyx subapical. Seeds long-tailed.

MEXICO: San Luis Potosi: Minas de San Rafael, *C. A. Purpus 4910* (A, F, G, US), *5368a* (G, MO, NY, US).

Unable to examine the type, the identification of this species is based on the original detailed description published by Körnicke and the diagnostic characters supplemented by Koehne who probably saw the type or an isotype. Körnicke described the species as having ovate or broad-elliptic leaves which are obtuse and apiculate or subacute at the apex, and about 3 cm. long and 1.5 cm. wide on sterile shoots. He did not mention the nature and position of the buds and the presence or absence of hairs on the style. For these characters we have to rely upon Koehne's observations. In his latest synopsis of the genus, under the subsection Gemmati which was characterized as having a smooth almost obsolete and glabrous style he placed *P. asperifolius* and *P. serpyllifolius* Gray. Judging from the style of the latter species, the type of which is before me, Koehne's characters indicate a species in which the styles are short but definitely present, 0.5–1.5 mm. long. By inference, Körnicke's description, which calls for no style and the stigmatic column thick and subsessile, may also be interpreted to apply to flowers with short but definite styles. One of the elements of *Purpus 5368*, which I have indicated as *5368a*, has small ovate leaves, 0.5–1.7 cm. long, 0.4–0.7 cm. wide on the flowering shoots, and glabrous styles. These characters conform to Körnicke's description of the leaves and Koehne's diagnosis of the style of *P. asperifolius*, thus I interpret that element as representing Körnicke's species. *Purpus 4910* is a poorly selected fruiting specimen. With the exception of one, all sheets I have examined are sterile, and the only fertile specimen has just one fruit with a broken top. The branching is much looser than is that of *Purpus 5368a*. The leaves seem to fit Körnicke's description of those on the vegetative shoots. The small part of the disc left on the broken fruit appears to be glabrous.

The ovate shape of the strigose leaves, the densely villose hypanthia and the very short pedicel of the flower of this species suggest a very close relationship with *P. coulteri* Wats. Yet it can be readily distinguished from Watson's species by its glabrous disc and style and its rather small leaves on the flowering shoots which are only 1–2 cm. long. *Philadelphus coulteri* Wats. has a pubescent disc and style, with the leaves on the flowering shoot 2–3 cm. long. The fragrant white flowers of this species appear in June.

12. **Philadelphus sargentianus**, sp. nov.

Philadelphus coulteri Wats. in Proc. Am. Acad. 22: 472. 1887, pro parte (quoad col. Sargent, excl. *Coulter 77*); et in Gard. Forest 1: 232, fig. 40.

1888. — Nicholson, Suppl. Dict. Gard. 594. 1900. — Rydberg in N. Am. Fl. **22:** 170. 1905. — A. H. Moore in Bailey, Stand, Cycl. Hort. **5:** 2582, fig. 2905. 1915. — Standl. in Contr. U.S. Nat. Herb. **23:** 311. 1922. — Rehder, Man. Cult. Trees Shrubs 280. 1927; ed. 2. 275. 1940; et Bibliogr. Cult. Trees, Shrubs 159. 1949.

Frutex usque 2.3 m. altus, ramis robustis, bienniis 3 mm. diametro, brunneis, longitudinaliter rimulosis, hornotinis 1.5 mm. diametro, dense hirsutis, pilis basi haud incrassatis, gemmis axillaribus conicis, strigosis, pilis luteis; foliis ovatis vel ovato-ellipticis, 2.5–4.5 (raro 5) cm. longis, 1–2 (raro 2.5) cm. latis, basi rotundatis, apice acutis vel obtusis, apiculatis, supra hispidis, subtus dense argenteo-villosis, 3- vel 5-nerviis, margine inconspicue serrulatis, dentibus utrinque 1 usque ad 5, minutis, petiolo 3–5 mm. longo; floribus solitariis, pedicellis brevissimis, 2–3 mm. raro ad 6 mm. longis, cum hypanthiis calycibusque dense albo-villosis; hypanthiis subglobosis, 5 mm. diametro, pilis longioribus et brevioribus intermixtis; sepalis ovatis, acuminatis, 8 mm. longis, 4–5 mm. latis; corolla usque 4.5 cm. diametro, petalis obovatis, 2 mm. longis, 1.6 cm. latis, apice erosis; staminibus ca. 40, antheris 2 mm. longis; disco medio piloso, stylo brevissimo, 1 mm. longo, stigmatibus 4 mm. longis, liberis; capsulis subglobosis, 1 cm. diametro; seminibus longe caudatis.

MEXICO: Nuevo Leon: Monterey, Sierra Madre Mts., Diente Canyon, *C. H. & M. T. Mueller 544*(A, F); *C. G. Pringle 2094*(A, NY, US); *C. S. Sargent* in April 1887(A TYPE; G, originally placed under *P. coulteri*); Cerro de la Silla, *S. S. White 1470*(G).

In the publication of *P. coulteri*, Watson cited two collections, *Coulter 77* from Zimapan and *Sargent s.n.* from Monterey. Watson's species was published in 1887. Sargent's specimen was collected in April of that year. It is highly possible that Watson had prepared the description of *P. coulteri* before he saw the Sargent specimen. When Sargent sent him his Monterey collection, Watson simply incorporated it in his new species. As the species was named for Coulter, his collection naturally becomes the type of *P. coulteri* Wats. But Sargent's collection is definitely different from the type of *P. coulteri* Wats. which has the rugose branchlets and strigose leaves, characteristic of species like *P. mexicanus* Schlechtendal. Sargent's material has villose branchlets and leaves hispid above and densely white villose beneath, a type of pubescence characteristic to the northern element like *P. madraensis* Hemsl. Yet Sargent's specimen is not Hemsley's species because of its exposed buds, and it is thus described as new here.

Philadelphus sargentianus is endemic to Monterey where it grows at altitudes of 1500–1600 meters, where the mean annual temperature is 62°–67° F. and the mean annual rainfall is limited to 30–40 inches. There its fragrant white flowers appear from early April to July. As far as I know this species has never been introduced into cultivation. Unfortunately misled by the publication of an illustration drawn on the basis of the Sargent collection, several authors of standard references on

the cultivated trees and shrubs had misinterpreted this species as *P. coulteri*.

13. **Philadelphus pringlei**, sp. nov.

Philadelphus coulteri sensu Brandegee in Univ. Calif. Publ. Bot. 4: 270. 1912, non Wats.

Frutex, ramis brunneis, bienniis 2 mm. crassis, longitudinaliter rimulosis, hornotinis 1.5 mm. diametro, dense hirsutis, pilis basi incrassatis, gemmis axillaribus conicis, pilosis; foliis ovatis, raro lanceolatis, 2.4–5 cm. longis, 1–1.8 cm. latis, basi rotundatis, obtusis, raro acutis, inconspicue triplinerviis, apice acutis, breviter acuminatis vel raro obtusis, apiculatis, inconspicue serratis, serrulis utrinque 2 usque ad 5, minutis argutisque, supra hispidis, subtus dense argenteo-villosis, petiolo 4–5 mm. longo; floribus solitariis, pedicellis 2–4 mm. longis, cum hypanthiis calycibusque dense albo-villosis; hypanthiis subglobosis, 5 mm. diametro; sepalis ovatis, 8 mm. longis, 5 mm. latis, acuminatis; corolla cruciformi, 4–5 cm. diametro, petalis obovatis, 2 cm. longis, 1.5 cm. latis, apice rotundatis; staminibus 40 usque ad 44, antheris oblongis, 2 mm. longis; disco glabro, stylo 4 mm. longo, glabro, supra diviso, stigmatibus 3–3.5 mm. longis; capsulis subglobosis, immaturis 7 mm. diametro.

MEXICO: Nuevo Leon: Sierra Madre, above Monterey, *C. G. Pringle 10174* (A, TYPE; F, G, MO, US, ISOTYPES); Diente Canyon, about 12 miles south of Monterey, *C. H. & M. T. Mueller 261* (A, F); Waterway below Alamar, about 15 miles southwest of Galeana, *C. H. & M. T. Mueller 656* (A, F, NY).

Geographically this species has the same range as *P. sargentianus* S. Y. Hu and morphologically they are very similar except *P. sargentianus* has a pubescent disc and style, while this species has glabrous ones. According to the collectors, this taxon is abundant in the open woods and shrub zones of the Sierra Madre Oriental in the state of Nuevo Leon. Its white flowers appear in April and May.

14. **Philadelphus calcicolus**, sp. nov.

Frutex usque ad 5 m. altus, ramulis teretibus, cinereis, bienniis 1.5 mm. crassis, corticibus clausis, hornotinis brunneis, 1 mm. diametro, pilosis, gemmis terminalibus conicis, strigosis, pilis luteis; foliis serratis, lanceolatis vel ovatis, 2.5–5 cm. longis, 1–2 cm. latis, basi acutis vel obtusis, trinerviis apice subacuminatis et apiculatis vel acutis, supra in sicco nigrescentibus, pilosis, subtus olivaceis, sparsissime villosis, petiolo 5–8 mm. longo; floribus solitariis, pedicellis 3–6 mm. longis, incanis, hypanthiis subglobosis, 6 mm. diametro, dense tomentosis, argenteis; sepalis ovatis, acuminatis, 7 mm. longis, basi 4.5 mm. latis, argenteis; corolla 3 cm. diametro, petalis obovatis, apice emarginatis, 1.5 cm. longis, 1.3 cm. latis; staminibus ca. 40, antheris sagittatis, 2 mm. longis; disco glabro, stylo brevissimo, 1.5 mm. longo, stigmatibus 4 mm. longis, cristatis,

coalescentibus; capsulis ellipsoideis, 8 mm. diametro, sepalis persistentibus 1/3 apicem insertis; seminibus breviter caudatis.

MEXICO: Nuevo Leon: Dulces Nombres, *F. G. Meyer & D. J. Roger 2662* (TYPE, MO; fragment A); Canyon above Linare toward Galeana, *A. J. Sharp 45787* (TENN. A, sterile). Tamaulipas: Road above Cindad Victoria toward Jaumave, dry canyon slope below 3000 ft., *Sharp, Shanks, Wolfe & Hernandez 52006*, (A, TENN).

This species grows on dry limestone cliffs above a dry stream bed at an altitude of 1300 meters. The white flowers appear in June. It is a very interesting plant for most of the lateral buds on the branchlets are weak, as a rule not visible, and do not develop in the following year. Often only those situated near the apices of the shoots, either the apical alone or the two axillary ones, develop into flowering or vegetative shoots. In this respect as well as by its short styles with long cristate stigmas, emarginate petals, and slender petioles this species resembles *P. osmanthus* S. Y. Hu. The latter species can be distinguished by its pubescent disc, less canescent hypanthium and calyx, and hairs with thickened bases on the stem. Its smooth appressed white indumentum on the hypanthium and calyx and its hairs on the stem not thickened at the base also suggest a relationship with *P. argenteus* Rydb., in the section Microphyllus of the subgenus Euphiladelphus. Rydberg's species can be distinguished by the enclosed buds and small entire leaves which are densely white pubescent beneath. The coalescent stigmas and the short caudate seeds also suggest some relationship with the southern Appalachian species *P. hirsutus* Nutt., but the latter species can be distinguished by its prominent axillary buds, the style longer than the stigmatic column, and the ecaudate seeds.

(*To be concluded*)

POLYPLOIDY AND APOMIXIS IN COTONEASTER

HALLY J. SAX

THE ROSACEAE have drawn the attention of investigators because of the variety and beauty of their flowers and fruits as well as their horticultural value. They are a large and varied family with a wide distribution. Many examples of polyploidy and apomixis have been reported in this family.

Of the four subfamilies of the Rosaceae, the Pomoideae are of special interest because of their allopolyploid origin. The basic chromosome numbers of the other subfamilies, the Rosoideae, Prunoideae and Spiroideae, are 7, 8, and 9. The basic chromosome number of the Pomoideae is 17, derived from primitive ancestors by hybridization followed by chromosome doubling.

The eighteen genera of the Pomoideae are rather closely related, as is shown by the fact that many generic hybrids occur in nature. Their close relationships are further supported by the readiness with which most of the genera can be intergrafted.

Many of the genera of the Pomoideae are characterized by secondary polyploidy, that is, the chromosome number in many cases has doubled again, this time probably by autopolyploidy. Secondary polyploidy is common in *Malus* and *Crataegus*.

The genus *Cotoneaster* is less well known than *Malus* and *Crataegus* of the same subfamily. In his "Manual of Cultivated Trees and Shrubs" Rehder (56) notes that there are about 50 species of *Cotoneaster* in the temperate regions of Europe, N. Africa and Asia (except Japan, where there are no native species). These are mostly shrubs, rarely small trees, with some beautiful prostrate forms among them. Their fruit is especially attractive: red, black, purple and a few orange pomes. They are planted often because of their brightly colored fruits as well as the flowers, which are in many cases small, white to pinkish and of many-flowered corymbs. There are also some evergreen and partly evergreen varieties, both upright and prostrate forms, which are very beautiful with the brilliantly colored fruit.

Plant collectors have brought many species of these Cotoneasters into cultivation. Their size, variety, and adaptive qualities make them desirable as ornamental plants. The relationship of these species is not very easily determined, and the Cotoneasters have been considered a difficult genus by the taxonomist.

The characteristics often show differences in size, hairiness, etc., but mostly intensification of some character predominating over that in another species, and often that is the only difference. In reading over the descriptions of the many species and varieties, as well as observing them

in the field, it becomes apparent why *Cotoneaster* is a difficult genus for the taxonomist. In describing *C. francheti* var. *sterneana*, W. B. Turrill (74) in 1950 remarks, "While we have not sufficient information to give full reason for this, since we do not know how far hybridization happens in the wild, how plastic are individual plants, or how much intraspecific genetic variations occur, there results frequent difference of opinion between 'lumpers' and 'splitters.' Splitters have been carried too much." He cites *Crataegus* and appeals to the cytogeneticist to study *Cotoneaster*.

POLYPLOIDY AND APOMIXIS IN THE ROSACEAE

Doubling of the chromosome number at the time of union of the egg and male nuclei followed by a reduction to half the number at the time the spore mother cells divide to form the megaspores and microspores is general throughout the plant kingdom. Asexual methods, such as root or stem cuttings, leaf and axillary bulbs, budding, etc., also occur, but these do not involve a doubling and reduction of the chromosome number; the offshoot carries the chromosome number of the organ from which it comes, while in sexual reproduction there is an alternating cycle between the haploid and the diploid number of chromosomes.

Many instances of changes, modifications of the usual behavior, or abnormalities have been found to occur in the development of the egg and male nuclei and in the development of the spores to form the gametophytes which produce the eggs and the male nuclei. Some of these, such as the functioning of a cell or cells of the integument of the ovary to form the embryo, or the direct development of a megaspore mother cell without reduction to form the spores, the development of an unreduced egg cell. do not involve a change in the chromosome number. These various substitutions for fertilization and meiosis are classified under the term apomixis. Parthenogenesis, apospory, apogamy, and vegetative buds are all included.

No attempt will be made to review all the literature on the subject of apomixis. The earlier work has been reviewed by several investigators, Ernst, 1918 (16) and others including Rosenberg (58) in 1930, who gave a summary of the work up to that time. Steil in 1939 (70) reviewed the literature on ferns. Then Stebbins (68) brought the review up to 1941 in his discussion on "Apomixis in the Angiosperms." The subject again underwent a thorough review by Gustafsson (31) in 1947. Subsequently many instances of apomixis have been reported, especially in connection with polyploidy. This work, as well as the extensive literature on polyploidy, will be discussed here only in connection with the work on the Rosaceae, of which *Cotoneaster* is a member.

The role of polyploidy and apomixis in speciation, evolution and geographical distribution is well illustrated in many genera of the Rosaceae. In general there is much variation in the appearance of apomixis and a relatively high frequency of polyploidy.

Much of the early work on polyploidy in relation to speciation was done

with the genus *Rosa* by Blackburn and Harrison (4) in 1921, Täckhohn (71) in 1922, and Hurst (36, 37, 38) in 1925, 1928, and 1932. A wide range of polyploidy was found, and Hurst attempted to classify the species of *Rosa* into five basic genomes. Crosses between the basic diploid species gave rise to the complexities of the polyploid species. Later cytological studies of this same group by Gustafsson and Häkensson (32) and Gustafsson (29) gave further information indicating that the cytogenetic relationships of the *Rosa* species are more complex with both auto- and alloploid as well as intermediate complexes. Fagerlind (18, 20) goes even further and suggests that segmental interchange between the chromosomes of the basic genomes leads to complex pairing relationships in triploids. Both Gustafsson and Fagerlind concluded that apomixis in *Rosa* was a species trait present in diploid species, and that the present association between polyploidy and apomixis is secondary.

Many of the North American species of *Rubus* were found to hybridize by Brainerd and Peiterson (5) in 1920 and Peiterson (52) in 1921. In the experiments, hybrids between different sexual species of *Rubus* (Peiterson, 52) and other genera have in no instances shown any clear indication of apomictic reproduction, even though the parental species are closely related to apomictic forms. Longley (43) in 1924 suggested that apomictic forms existed. In 1930 Gustafsson (25) reported unreduced pseudogamy in a species of *Rubus*. In some cases of pseudogamy the number of apomictic and sexual offspring vary according to the chromosome number of the pollen parent. Darrow and Waldo (11) 1933, reported that the fertilization of a tetraploid species of *Rubus* with pollen from a diploid species yielded a majority of sexual offspring; but it and other tetraploid apomicts produced few or none with pollen from tetraploid species. Crane (7) obtained similar results when using pollen from a diploid form of *R. idaeus* on an octaploid species of *R. vitifolius*; only pentaploid hybrids were produced. When he used pollen from the tetraploid form of the same parent, hybrids and matriclinous octoploid offspring resulted. Pollen from the hexaploid *R. loganobaccus* (2 n = 42) produced only hybrids. Petrov (53), using pollen of the hexaploid *R. loganobaccus* on a triploid with unreduced eggs, obtained hexaploid hybrids; but using pollen of a triploid, *R. idaeus*, only triploid pseudogamous progeny result.

Although polyploidy is common in the genus *Rubus*, Gustafsson (27, 28) found apomixis was confined to only one section. As in *Rosa*, many of the species are facultative apomicts.

Many of the facultative apomicts are heterozygous, and Haskell (34), 1953, has suggested that another factor in the variation of *Rubus* may be crossing over at meiosis in the production of an unreduced egg cell. In *Rubus* crosses between two facultative apomicts give sexual progeny.

The genus *Potentilla* has also provided evidence regarding the role of polyploidy in evolution and speciation (Claussen, Keck and Hiesey 6), 1940, and the role of apomixis. *Potentilla* species (Müntzing 46 and 47) showed variation in the development of the microspore mother cell. Meio-

sis was regular in the microspore mother cell of *P. argentea* but irregular in *P. collina* and *P. hirta*. *Potentilla argentea* is apomictic through facultative apospory. The embryo may develop autonomously. Similar results were reported by Popoff (55), Gentcheff (23) and Gentcheff and Gustafsson (24). The genetic studies of Müntzing and Müntzing (49) on reproduction between sexual and apomictic forms indicate that apomixis is controlled by multiple factors.

Among the Prunoideae the genus *Prunus* has been studied extensively. Meurman (45) in 1929 reported a high polyploid species, *Prunus laurocerasus* L. with eighty-eight chromosomes. Polyploidy is common in *Prunus*, and the allopolyploid origin of *P. domestica* was determined by Rybin (59) in 1936. According to Almeida (1), *P. lusitanica* is an octopolyploid with 2 n = 64, an allopolyploid of ancient origin behaving like a diploid. Cytological work by Schelhorn (65) showed great irregularity in the nuclear divisions and tetrad formation in a triploid of *P. avium*, which the author believes arose by the fertilization of an unreduced sexual cell of *P. avium* with a sexual cell, and not as a cross of *P. avium* and *P. cerasus*.

The basic diploids show considerable stability of the genome, as is evidenced by the regular meiosis and high fertility of the hybrid between *P. tomentosa* from China and *P. besseyi* from Central North America (Sax unpublished). Apomixis has not been found in this subfamily.

Little cytological work has been done on the Spiroideae, but both autopolyploidy and allopolyploidy have been found in *Spiraea*, Sax (64). Polyploidy appears to be related to geographical distribution, since the Old-World species are largely diploid while most of the American species are late-flowering tetraploids.

The Pomoideae are unique in that the subfamily is of allopolyploid origin. Secondary polyploidy is common in most of the genera, and triploids play an important role in both natural and cultivated species. Polyploidy has complicated the genetic and taxonomic variation of most of the genera and in a few cases is related to geographic distribution.

The first extensive work on the genera of Pomoideae was done by Longley (42) in 1924. He determined the chromosome number in eighty species of *Crataegus* from the collection in the Arnold Arboretum. He found thirteen diploids, sixty-seven triploids, and ten tetraploids.

The chromosome relationship in the Pomoideae was studied by Sax (62 and 63). In the Rosaceae the subfamilies, the Rosoideae, Prunoideae and Spiroideae, have basic chromosome numbers 7, 8 and 9, while the Pomoideae have 17 as the basic chromosome number. The close relationship among them suggests that they originated as a cross between primitive ancestors of the other Rosaceae.

Dermen (12) in 1936 discovered in *Malus hupehensis* a delayed development of the embryo from the unreduced egg after the flower opened.

Johansson (39) suggested that there were four places of fruit origin: the Caucasian region, the Turkestan region, the East Asiatic region in-

cluding East Siberia, and North America. The new varieties arose through crossing, mutation, and doubling of the chromosome number.

Polyploidy in *Malus* has been studied by several workers. Einset (13, 14) found spontaneous polyploids among apple seedlings. Einset and Inhofa (15) also described periclinal chimeras; partly diploid, partly tetraploid, in apples. Hemming (35) discusses the origin of apples and the relation of diploid, triploid, and tetraploid species.

Some correlation has been shown between geographical distribution and polyploidy. Hägerup (33) in 1931 postulated an increase in the frequency of polyploidy with the increase in latitude. The results of studies by Tischler (73) of the frequency of polyploids at different latitudes in Sicily, Schleswig-Holstein, the Faeroes and Iceland supported that hypothesis. Further corroboration came from Flovik (22) in his investigations of the flora of Spitzbergen, all glacial survivors.

Gustafsson (26), Babcock and Stebbins (2), and Stebbins and Babcock (67) have found apomicts to be excellent material for studying the effect of environment on the genotype and the tracing of plant migrations. The distributional center of the American *Crepis* complex was found in northeastern California. Fernald (21), followed by Babcock and Stebbins (2), also considered the Appalachians to hold the ancient American *Antennaria* complex. Gustafsson (28) has made similar studies of *Taraxacum* and *Rubus* in Scandinavia. Curtis (9) also used apomicts in *Taraxacum* in England for the study of the effect of environment on the genotype.

Other literature on the subject of plant distribution was reviewed by Löve and Löve (44) in their work on "The Geographical Significance of Polyploidy." They conclude that polyploidy increases with the increase in latitude or the extremeness of the Pleistocene or post-glacial climate. The estimated frequency of polyploidy in the temperate zone is 30 per cent or lower.

COTONEASTER

In the present work the chromosome numbers of most of the species in the genus *Cotoneaster* were studied. It was hoped that this would show something concerning the relationships of some of the species, whether or not the species were polyploid, and give evidence as to whether there existed in this genus some of the irregularities in reproduction found in other genera of the Rosaceae as in *Malus* and *Crataegus*.

The presence of apomixis was also tested. Each season the flowers on some of the branches of a few species were destyled and emasculated while in the bud on some of the plants to see if they would produce fruit without fertilization; and if, as has been found in the apples, the development of the embryo could take place independently of fertilization by development from some part of the ovule. There are only a few species in which this work was done. Since only positive results were conclusive because in a few cases no fruit was set on the controls or occasionally on the entire plant, these results will be mentioned in connection with the species.

Seed from some of the species were planted to compare the progeny from the same seed source, to observe their resemblance to the parent plant, and to determine the proportion of hybrid plants occurring in natural populations.

The Cotoneasters in the Arnold Arboretum are all introduced species from Europe, Asia, and Africa. A few of these species were obtained from crosses made in cultivation; others were collected and brought into cultivation. The source of the species was usually known, especially the immediate place from which it was introduced. In most cases the plants came directly from their place of origin. The Arnold Arboretum's own collector, Ernest Wilson (75) brought seeds and plants from Asia directly to the Arnold Arboretum. Many of them bear the authority of Rehder and Wilson. In other cases seeds have come from well-known plant explorers in England, France, Germany, Holland, China, and India, and other equally familiar sources elsewhere and in the United States.

The material for the present work was collected during the spring and summer of the years 1950 through 1954 and was confined to the species available in the Arnold Arboretum. This included most of the well-known species, as may be noted from the list given in the table (Table I), although not all the varieties of each species were studied. There were a few plants labeled "C. sp." denoting the difficulty in naming them, and as mistakes in labeling may occur in the best collections, the number on the metal label on each specimen was copied for further tracing if necessary. All were checked with the specimens in the herbarium of the Arnold Arboretum.

The Cotoneasters blossom over a fairly long period in the spring, but it is necessary to obtain the dividing microspore mother cells at the right stages in division. During a particularly warm day most of the buds on a plant might pass through the division stages. In some species where new buds are produced over a longer period, material is more easily obtained. The difficulties of fixing such a large number of varieties in a short time meant that some were missed some years. In some rare cases the plants were not in flower every year or they were newly planted. The size of the flower bud when the divisions occurred differed in the various species. However, most of the available species, though not all, were obtained when the divisions were in progress each season, and the results were determined and checked. All those reported were checked at least two seasons, and many were studied four or five seasons.

The buds were fixed in alcohol acetic solution twenty-four hours, then changed to 95% alcohol. These were left under refrigeration until aceto-carmine smears of the pollen mother cells could be made and studied.

The chromosomes in the Cotoneasters are small, but there was an abundance of material and in practically all cases it was possible to obtain well-fixed material at all stages.

In the study of the chromosome numbers it was noticeable that the chromosome pairing was quite characteristic for any given species. In many of the species there was a tendency for the sets of chromosomes to

adhere strongly in the late prophase and metaphase, and at these stages in many cases the count would be 17 or thereabout even when the form was triploid or tetraploid except for a few univalents. The chromosomes in these cases would appear unusually large for *Cotoneaster*. However, as the chromosomes separated and were counted in the anaphase stage, it was apparent that the species were often triploid or even tetraploid.

The diploids are very regular in their divisions. The 17 small chromosomes pass to the poles and are easily counted. The polyploids were not so easily counted in all cases, but they had a very characteristic appearance. The chromosome complex was larger and the pollen mother cells were usually so much larger that they suggested polyploidy after one became familiar with them. This did vary somewhat, but in all the diploids studied the pollen mother cells were smaller than in most polyploids; exceptions were noted in the polyploids.

Univalents were very often present in the dividing nuclei of the polyploids. The triploids showed chromosome bridges and other irregularities. The chromosome count varied according to the closeness of adherence of homologous pairs. Often pieces of chromatin, even whole chromosome bridges were left outside in the cytoplasm. As many as twelve such chromosome remnants were counted, but usually two to six were found outside in the cytoplasm. These were visible after the daughter nuclei had rounded up in the later stages. Tetraploids were less irregular, although univalents were often present. The number was obviously larger, and when they separated the counts showed the tetraploid number. At time some of the univalents were lost in the cytoplasm.

The counting of the chromosomes in the polyploids is complicated by an early loosening of the arms of the V-shaped chromosomes as they near the poles, which makes it appear as a larger number of chromosomes if the two arms are counted separately.

In every species the counts were checked from the same slides by Professor Karl Sax, to whom I wish to express my thanks.

The results of these studies are given in Table I. The species are listed in alphabetical order.

TABLE I

COTONEASTER

Species and Variety	Habitat	Zone	Chromosome Number
C. acuminata Lindl. 226–39 *	Himalayas	5	2 n
C. acutifolia Turcz. 15686	N. China	4	2 n
C. acutifolia ? 2291	Tao Basin		3 n
C. acutifolia var. *villosula* Rehd. & Wils. 13165B	Cent. & W. China	5	4 n

* Numbers refer to Arnold Arboretum accession numbers.

Species and Variety	Habitat	Zone	Chromosome Number
C. adpressa Bois 7951	W. China	4	3 n
C. adpressa hessei 813–41			3 n
C. adpressa var. *praecox* (Vilm.) Bois & Berthault. 134–18			3 n
C. affinis var. *bacillaris* (Lindl.) Schneid. 17806–A & B	Himalayas	7	4 n
C. ambigua Rehd. & Wils. 134–22	W. China	5	3 n
C. apiculata Rehd. & Wils. 7275	W. China	4	3 n
C. bullata Bois 861–32A	W. China	5	3 n
C. bullata f. *floribunda* (Stapf) Rehd. & Wils. 6685–2	W. China		3 n
C. bullata var. *macrophylla* Rehd. & Wils. 13426	W. China		3 n
C. conspicua Marquand 1019–36C	W. China	7 ?	2 n
C. dammeri Schneid. 137–51	Cent. China	5 ?	2 n
C. dielsiana Pritz. 686–33	Cent. & W. China	5	3 n
C. dielsiana Pritz. 134–28A & B			3 n
C. divaricata Rehd. & Wils. 6587C	Cent. & W. China	5	3 n
C. foveolata Rehd. & Wils. 13431A & B	Cent. China	4	3 n
C. francheti Bois 130–32D	W. China	6 ?	4 n
C. frigida ? Lindl. 191–40	Himalayas	7	2 n
C. froebelli Vilmorin 757–30B	Cult.		3 n
C. glabrata Rehd. & Wils.	W. China	7	2 n
C. glaucophylla Franch. 571–36	W. China	7 ?	3 n
C. henryana Rehd. & Wils. 223–07	Cent. China	7 ?	2 n
C. horizontalis Decne. 45–34	W. China	4	3 n
C. horizontalis var. *perpusilla* Schneid. 7157A	W. China		3 n
C. horizontalis var. *prostrata* 1070–38			3 n
C. integerrima Med. 1776–3, 1766B	Europe, N. Asia to Altai	5	3 n
C. lindleyi Steud. 372–37–A	Himalayas	6 ?	3 n
C. lucida Schlecht. 3284A & B	N. China, Mongolia Altai Mts.	4	3 n
C. melanocarpa Lodd. 6679–1	Europe to Cent. & N.E. Asia	4	4 n
C. melanocarpa var. *commixta* Schneid. 656–33			4 n ?
C. melanocarpa var. *laxiflora* (Lindl.) Schneid. 13490–1A	Cent. Asia		3 n
C. microphylla Lindl. 22906	Himalayas	5	2 n
C. moupinensis Franch. 13497A & B	W. China	6 ?	3 n
C. multiflora Bge. 21976, 14916	W. China	5	4 n

Species and Variety	Habitat	Zone	Chromosome Number
C. multiflora var. *calocarpa* Rehd. & Wils. 6679–1 & 2	W. China		3 n ?
C. multiflora var. *granatensis* (Boiss.) Wenz.	Spain	6	3 n
C. nitens Rehd. & Wils. 6681	W. China	4	3 n
C. obscura Rehd. & Wils. 6686–1	W. China	5	3 n
C. obscura var. *cornifolia* Rehd. & Wils. 11261A & B	W. China		3 n
C. racemiflora var. *desfontaini* (Reg.) Zab. 389–34	S. Eur., N. Afr., W. Asia to Himalayas and Turkestan	4	3 n
C. racemiflora var. *soongorica* (Reg. & Herd.) Schneid. 16428. 21846	W. China	3	3 n, 4 n
C. racemiflora var. *veitchii* Rehd. & Wils. 20075	Cent. China		3 n
C. rosea Edgew. 44939	N.W. Himalayas. Afghanistan	5	3 n
C. rotundifolia Lindl. 405–36A	Himalayas	6 ?	3 n
C. rubens W. W. Sm. 21991B	W. China	6 ?	3 n
C. salicifolia Franch. 434–33A	W. China	6 ?	
C. salicifolia var. *rugosa* (Pritz.) Rehd. & Wils. 458–36–A	Cent. China	5	3 n
C. schneideri 574–38–B			4 n
C. simonsii Bak. 596–33	N.W. India. Khasia	5	3 n
C. sp. H. Hesse 13492			3 n
C. sp. 524–30A & B			3 n
C. sp. 114–36B	China (Lu Shan Arb.)		3 n
C. tenuipes Rehd. & Wils. 7276A–C	W. China	5	3 n
C. tomentosa (Ait.) Lindl. 23–42–4A, 13507–1	S.E. Europe, W. Asia	4	3 n
C. wardii W. W. Sm. 659–33	S.E. Tibet	7 ?	3 n
C. zabeli Schneid. 7019B	Cent. China	4	3 n
C. zabeli var. *miniata* Rehd. & Wils. 7343D, 156–85	China		3 n

Triploid and tetraploid Cotoneasters are apt to be more vigorous than the diploids — but there is much variation among these; some are less vigorous. Often the main differences given in Rehder's Manual between some of the species and varieties is in vigor, intensity of color, size of flowers, leaves and fruit, pubescence, or looseness of inflorescence. There are other differences between species, but these are much the same variations existing between known diploid and triploid or polyploid species derived from them.

Cotoneaster acuminata Wallich is one of the first species described (Flora, 1823). It is a diploid species from Zone 5 in Nepalia in the

Himalayas (Table I.) A natural hybrid between this species and *C. acuminata* was collected by R. N. Parker. *Cotoneaster acuminata* is found along the Himalayas to Calcutta.

According to the table (Table I) the chromosome count for *Cotoneaster acutifolia* Turcz. is 17. The pollen mother cells were small. It is a diploid and its natural habitat is N. China. It has been found on a mountain near Peking by Bretschneider. Specimens in the herbarium from various localities in northwest China at high altitudes are labeled *C. acutifolia* Turcz. Wilson (75) says there is no typical *acutifolia* in China proper. but in Mongolia, but that there are two well-marked varieties in central and west China.

Another plant labeled *C. acutifolia* (?), carrying a different number. was grown from seed collected by Joseph F. Rock in the Tao River Basin, Kansu Province, China. It is obviously a different variety with a triploid chromosome count and lagging chromosomes. This is a triploid probably derived from *C. acutifolia* Turcz.

One of the varieties, *C. acutifolia* var. *villosula* Rehd. & Wils., is found in Central and West China. This is a polyploid and was recognized as a new variety by Rehder and Wilson (56). It is described as "densely villous beneath, somewhat larger; calyx tube more densely villous; fruit thinly pubescent." From the chromosome counts this was considered a tetraploid, although there was some irregularity.

Closely related to *C. acutifolia* Turcz. is *C. ambigua* Rehd. & Wils. from West China which, according to Rehder's Manual of Cultivated Trees and Shrubs (56), "differs chiefly in its slightly pubescent or nearly glabrous calyx tube and subglobose fruit with three to four nutlets." *Cotoneaster ambigua* is a coarser plant in general and more rigid in appearance than *C. acutifolia* Turcz. and bears a closer resemblance to *C. acutifolia* var. *villosula* Rehd. & Wils., but on comparison of the two plants side by side in the field they appeared sufficiently different to be separate species. In Plantae Wilsonianae, Wilson (75) makes the remark, "In speaking of ambigua, it is noted that all acutifolia like specimens are grown in the arboretum and later it may be possible to determine their relation to each other." *Cotoneaster ambigua* is a triploid. The divisions of the nucleus in the pollen mother cells are irregular with bridges still holding at anaphase and scattered univalents. The homologues show some tendency to adhere. The pollen mother cells often did not finish dividing but decomposed at some stage in their development. There was also much variation in the stages in an anther and much decomposition in the pollen mother cells. *Cotoneaster ambigua* produced fruit. The specimen in the Arnold Arboretum was heavily fruited in 1953, suggesting apomixis in such an irregular triploid.

Cotoneaster tenuipes Rehd. & Wils. is also noted as a species closely related to *C. acutifolia* Turcz. It has a very graceful fine slender development throughout and would not be mistaken for either *C. acutifolia* var. *villosula* or *C. ambigua*. It is less coarse even than the diploid species *C. acutifolia* Turcz. *Cotoneaster tenuipes* is a triploid form which has smaller

chromosomes and pollen mother cells like those of the diploid, but the chromosome number is higher than the basic number for the genus. There were chromatin bridges and fragments in the cytoplasm at anaphase. Although the pollen grains were smaller, like those of a diploid, it was obviously a triploid or aneuploid. There was little mature fruit on the plant in the years 1950–1952, but it was well fruited in 1953. It is probably apomictic.

Cotoneaster tenuipes Rehd. & Wils. grew in West China, as did *C. ambigua* Rehd. & Wils. and *C. acutifolia* var. *villosula* Rehd. & Wils., the latter extending into central China. The two former are triploids, the latter a tetraploid. They grew in Zone 5 (i.e. Rehder's Map of Climatic Zones), while *C. acutifolia* Turcz. was found in Zone 4 and in North China.

There must be some relationship between them, as they have similarities that the systematist recognizes. There is the possibility that the triploids just mentioned came from a cross in which *C. acutifolia* was one of the parents, or that the chromosome number of *C. acutifolia* had doubled in number, forming a tetraploid (var. *villosula*) and then back-crossed with *C. acutifolia* or another diploid, giving triploids. Their distribution would support this assumption.

Cotoneaster lucida Schlecht. was once labeled *C. acutifolia* Lindl. (not Turcz.). It came from the Altai Mountains in Mongolia, Zone 4 (North China). It is quite different from *C. acutifolia* Turcz. *Cotoneaster lucida* has larger glossy and lustrous leaves. It is a triploid. It may be that this species has some relationship to *C. melanocarpa* as well as *C. acutifolia*.

Cotoneaster foveolata Rehd. & Wils. is represented by two vigorous specimens in the Arboretum grown from the same collection of seeds. They are alike. *Cotoneaster foveolata* is a large stiff shrub with large leaves. It is a triploid with much irregularity in the nuclear divisions of the pollen mother cells. Pieces of chromatin are left out in the cytoplasm after the dividing nuclei are formed. *Cotoneaster foveolata* comes from central China, Zone 4.

Cotoneaster moupinensis Franch. is a large stiff shrub which, like *C. foveolata*, has a rigid appearance. Rehder describes it as "similar to C. bullata but with black fruit." It comes from western Szechuan, West China, at 1300–2000 m. altitude. It is common in woods and thickets. It is a triploid. Wilson comments about the series as follows: "It must be confessed, however, that there is a great similarity between all these black fruited Cotoneasters from China." He noted that there were only slight variations between these *acutifolia*-like species and that they could be arranged in a gradual series. He believed that since they are all cultivated in the Arnold Arboretum someone may later determine their affinities and find the relations of the *acutifolia*-like ones.

Cotoneaster bullata Bois and its variety *C. bullata* var. *macrophylla* Rehd. & Wils. are among the most attractive shrubs in the Arboretum in the autumn because of their large clusters of abundant brilliant red fruits and very healthy dark green leaves. The *macrophylla* variety is especially

striking, having a larger leaf and inflorescence. Wilson says that *C. bullata* is a comparatively rare plant, though scattered over wide areas in Szechuan. It is found in open conifer forests in southeastern Tibet at 9000–10000 feet, inhabiting Zone 5 — a zone adjacent to that of *C. moupinensis*, which is in Zone 6 in that same area. *Cotoneaster bullata* Bois is a triploid. The division of the nuclei of the pollen mother cells was very irregular, with twenty-two to twenty-eight chromosomes, depending on the looseness of pairing. There were chromosome bridges and many univalents, up to as many as twelve in one anaphase.

The variety *C. bullata* var. *macrophylla* Rehd. & Wils. is also a triploid; univalents, bivalents, and trivalents are present. It is very irregular, with chromosome bridges at anaphase.

Another form, *C. bullata* f. *floribunda* (Stapf) Rehd. & Wils. is very attractive. It also has a triploid number with univalents and lagging chromosomes, but its homologues seem to be more closely paired. Under his remarks Rehder includes *C. moupinensis* var. (Stapf) as a synonym. It seems significant that this form *C. bullata* f. *floribunda* was described as *C. moupinensis* var. Stapf. It has bright red berries. *Cotoneaster bullata* f. *floribunda* is also found in the thickets of Szechuan, China. It is possible that *C. bullata* and varieties came from similar parental ancestry as *C. moupinensis*.

Very bright red berries with intensely green foliage and an attractive low habit characterize *C. apiculata* Rehd. & Wils., which grows in West China. This is a triploid with chromosome bridges and other irregularities in the reduction divisions in the anthers. In the late anaphase there are chromosome fragments left in the cytoplasm. Rehder gives *C. apiculata* as nearly related to *C. disticha* Lange, which ranges from the Himalayas to southwest China. (The latter was not in the Arboretum collection except for small cuttings, and it is not included in the counts. Counts on leaf-tip smears show that it is not a diploid.) There were three plants of *C. apiculata* grown from seed collected from the type plant by Wilson in China. They were alike. George Graves raised twenty-five plants from seed collected in the Arboretum. All were alike. The same was true of twenty-nine seedlings grown in the greenhouse, making a total of fifty-seven seedlings from the same original source.

Cotoneaster Lindleyi Steud. is a triploid. It produced no fruit 1950–1952, although it had some flowers on it in 1950 and 1951. In 1953 it flowered abundantly and produced fruit. This fruit became a deep lavender or bluish purple as it developed (much like that of *C. affinis* var. *bacillaris*) and gradually turned a purple brown and finally black — a word used by Rehder. Rehder includes *C. Lindleyi* as a species closely related to *C. racemiflora* (Desf.) K. Koch. It is a conspicuous species with its broad oval to broad ovate leaves rounded at the base. It came from the Himalayas (Rehder, Zone 6). It was very susceptible to fire blight.

Cotoneaster affinis var. *bacillaris* (Lindl.) Schneid. is probably a tetraploid. There were seventeen large tetravalent chromosomes in early equa-

torial plate stage and double that number at anaphase. Like *C. affinis* Lindl., which is not in the Arboretum, it is said by Rehder (56) to be closely related to *C. frigida*.

Cotoneaster frigida Lindl. is a diploid having seventeen chromosomes. Our specimen of *C. frigida* is quite different from the upright type described as typical. It lies flat on the ground with branches very stiff, like the one collected at Darjeeling. Some fruit set on the two destyled branches. The fruit is large and of a bright red color quite unlike that of *C. affinis bacillaris*. The latter is found in the Himalayas, as is *C. frigida*. They grow in Zone 7 (Rehder).

It is probable that *C. affinis* var. *bacillaris* came from the doubling of the chromosome number in *C. frigida* or a cross between *C. frigida* and some other form. There is quite a noticeable similarity between *C. affinis* var. *bacillaris* and *C. lindleyi*, which is a triploid. *Cotoneaster lindleyi* may have come as a backcross from *C. affinis* var. *bacillaris* and a diploid. There are several diploids in that region.

In writing of the variety *C. dielsiana* var. *elegans* Rehd. & Wils., Wilson remarks on the herbarium sheet that "this western plant shows marked differences from the type . . . in several respects approaching *francheti* Bois. It also has affinity with *C. Zabeli* Schneider. Its thinner yet more persistent leaves, smaller pendulous fruit, brick and orange red, distinguish this variety from the typical form." It is found in thickets 3500–4000 feet on the eastern slope of Likiang snow range, Yangtze Watershed, Szechuan. These observations are supported by a study of the chromosomes.

There are three specimens of *C. dielsiana* Pritz. in the Arboretum. One (*C. dielsiana* 686–33) was from the United States Department of Agriculture. After *C. dielsiana* was fixed two years in succession, a difference in the behavior of the chromosomes was noted for the two years. A check of the numbers showed that the material had come from the other two plants the second year. These two plants were grown from seeds labeled *C. dielsiana* 134–28–A & B, which were collected by Wilson in China, and they are alike. The fruit of this specimen is red and waxy and the leaves have color in the fall. It fits the description by Rehder. The fruit of the U. S. D. A. specimen is a reddish yellow fruit like that described for the variety *elegans*. *Cotoneaster dielsiana* (686–33) varied in the chromosome counts, depending on the looseness of pairing of the homologues. There were univalents, bivalents, and trivalents. Bridges were present in the anaphase stage. This is undoubtedly a triploid.

The chromosome counts from the specimens grown from the seed from China (134–28) appear to be 17 and up to about 21 in equatorial plate stage, depending on looseness of adherence. In the first anaphase the count appears to be higher than it appears at metaphase, and univalents and stragglers are apparent. The second anaphase counts are 17 and higher with irregularities. This may be an aneuploid.

George Graves grew a thousand seedlings from seed collected in the Arnold Arboretum. They were uniform in habit and growth like the 673

seedlings from 134–28 grown in the greenhouse. They are undoubtedly apomicts, as there were many kinds of Cotoneasters growing near by.

There were five specimens of *C. divaricata* Rehd. & Wils. growing from a collection of seeds from China. There were no discernible differences between these. George Graves grew two hundred seedlings of *C. divaricata*. They showed no variation.

Cotoneaster divaricata is a triploid species with lagging chromosomes and univalents. It is very probably an apomictic triploid.

There are several varietal forms of *C. racemiflora* (Desf.) K. Koch (in the Arnold Arboretum) which are quite widely distributed in their origins and show much variation. They are found in southern Europe, North Africa, western Asia to the Himalayas and Turkestan. *Cotoneaster racemiflora* (Desf.) K. Koch is described by Rehder (56) as "a variable species, the typical form variety *C. racemiflora* var. *desfontaini* (Reg.) Zab. (var. *typica* Schneid.) has generally elliptic acutish leaves, while variety *nummularia* Dipp. has broader usually obtuse leaves."

The divisions of the nucleus of the pollen mother cells in *C. racemiflora* var. *desfontaini* (Reg.) Zab. are fairly stable in appearance, but there are some univalents and bridges in both divisions and some chromatin left out after the daughter nuclei are formed. The pollen mother cells and the chromosomes are large for the genus and the chromosome count shows that it is polyploid, probably a triploid, the homologues pairing loosely.

Some fruit set on the destyled pistils in *C. racemiflora* var. *desfontaini*, but only on some of the destyled branches. However, when set, the fruit was abundant on the destyled branches as well as on the controls.

Cotoneaster racemiflora var. *soongorica* (Reg. & Herd.) Schneid. from West China is represented in the Arboretum by two plants from different sources. They are growing side by side. The fruit of one, which came from the Framingham Nurseries, is a little darker in color, maturing a little later than the other, which was grown from seed (Hort. Judd). They both appear to be triploids, but there are some differences in their chromosome behavior. In the plant raised from seed there appeared to be a higher chromosome number. Perhaps the homologues were more easily separated. One of the obvious phenomena noticed in both cases — but especially in the plant from the nursery — was the large number of examples of the stages where the homologues were pulled apart along the plate but still adhering. The whole complex would be in that condition with several univalents and bivalents less regularly placed.

Cotoneaster racemiflora var. *veitchii* Rehd. & Wils. from Central China possessed the number of chromosomes and the irregularities of a triploid.

Cotoneaster rosea, another triploid, has attractive small pink flowers in glabrous three- to nine-flowered cymes. It comes from the northwestern Himalayas and Afghanistan. It is probably a facultative apomict, as it hybridizes at times with *C. acuminata*, according to Parker's notes on the herbarium sheet. Its branches are slender. It is supposed to be related to *C. racemiflora*, as shown especially by its fruit.

Cotoneaster multiflora Bge. is a very graceful shrub from western

Szechuan. It is handsome in bloom and it has attractive red fruits. This is a tetraploid. The counts are around 34. Late anaphase shows a larger count, which is characteristic, as the two arms of the chromosome separate further in the reorganization of the daughter nuclei. The divisions are fairly regular. Although *C. multiflora* grows in West China, the Arnold Arboretum Herbarium has also a specimen from Kashmir. This may be a variety of *C. multiflora* or of *C. racemiflora*.

Cotoneaster multiflora var. *calocarpa* Rehd. & Wils., with rosy-colored blossoms, shows much irregularity. It is probably a triploid, although at times it appeared to have too many chromosomes. They may be the homologues prematurely separated.

Cotoneaster multiflora var. *granatensis* (Bois.) Wenz. is a triploid, the chromosome counts varying with many univalents — as many as fifteen in one case. The homologues varied in the ease with which they separated. In some cases the division went no further than the pollen mother cells. There was much sterility. The pollen mother cells, as well as the chromosomes, were large.

Among the unidentified species *Cotoneaster* sp. Hesse 13492G is a triploid. The two unnamed specimens collected by Dr. Rock are also triploids. They are alike and came from the same collection of seeds.

It was found that two collections labeled *C. obscura* and collected at different times yielded different results as far as behavior of chromosomes was concerned. One of these gave results similar to those obtained from the material labeled *C. obscura* var. *cornifolia*. A survey of these specimens in the field showed the two latter to be similar, and a checking of the numbers carried by these shrubs against the cards in the files disclosed that the plants had come from the same collection of seeds! (The large label on the questionable plant had omitted the varietal name.) *Cotoneaster obscura* var. *cornifolia* Rehd. & Wils. is a triploid, as it is very irregular with univalents, lagging chromosomes, and irregular pollen size. *Cotoneaster obscura* is also a triploid, but it has fewer chromosomes and is somewhat less irregular in its divisions. The homologues may adhere more closely or it may be an aneuploid. It is not as coarse in general, having smaller leaves, more delicate branches, and dark red fruit, while the variety *cornifolia* has a purple-black fruit. These are both from West China. They are probably apomictic triploids related to *C. acutifolia* or a cross between *C. acutifolia* var. *villosula* and some diploid.

Cotoneaster francheti Bois and *C. schneideri* appear to be identical or nearly so. The appearance and behavior of the chromosomes first called my attention to the similarity. When the plants were checked in the field, they were almost identical. The red fruit of *C. francheti* Bois was a bit more deeply colored than that in *C. schneideri* which was orange-red. The latter, however, although located near by, is more shaded by other plants. It could, of course, be an apomict which is a "clonal variety" with very slight differences. Rehder (56) does not mention *C. schneideri*. The plant in the Arnold Arboretum came as seed from California. *Cotoneaster francheti* is a tetraploid species. It comes from West China.

Rehder comments on the similarity between *C. francheti* Bois. and *C. wardii* W. W. Sm. The leaves of *C. wardii* are larger and in general the bush is more vigorous. It looks quite different. The fruit is larger and red without the orange-red tint noticeable in the red of *C. francheti*. The chromosome behavior is different. *Cotoneaster wardii* is a triploid, probably with *C. francheti* as a parent. This may be a case where the triploid is more pronounced in various ways than the tetraploid.

Two plants of *C. simonsii* in the Arboretum come from different sources; one from seed from Wageningen, Holland, the other as a plant from a nursery. They are not exactly alike in chromosome behavior, one being more irregular with long bridges stretching from pole to pole in the anaphase and with many univalents. The other is a little less irregular, but the chromosome count is the same. Both are triploids according to chromosome count and behavior. The plants vary somewhat, too. The fruits of one are almost always solitary or in a small cyme; the other fruits are in a cyme. The one with solitary fruits is much like the variety *newryensis*, nearly related to *C. francheti*. A total of 384 seedlings of *C. simonsii* gave three variants.

Cotoneaster zabeli Schneid. is represented by four specimens — all from the same collection of seeds. They are alike. *Cotoneaster zabeli* is a triploid. In the third year of the experiment fruit was borne on the destyled branch.

Cotoneaster zabeli var. *miniata* Rehd. & Wils. is a smaller, more delicate variety in habit and flower, with a light orange-scarlet fruit instead of the bright red borne by *C. zabeli*. It is also a triploid. This, like *C. tenuipes*, was expected to be a diploid. It may be an aneuploid, as the count is low for a triploid.

Cotoneaster tomentosa (Ait.) Lindl. is represented by two plants in the Arboretum. They are alike. Each year the flowers on several branches were destyled while in the bud. These set fruit in about the same proportion as on the controls. Apomixis is very definitely shown here. These plants continue to flower all summer up to frost time; only a few flowers are in blossom on each branch at a time. *Cotoneaster tomentosa* is a triploid.

Rehder (56) speaks of *C. tomentosa* being similar to *C. integerrima*, but larger in every part and more pubescent. *Cotoneaster tomentosa* is distributed throughout Europe and West Asia in Zone 4 (Rehder).

One specimen is reported from Kansu, but it may differ and should be compared, as no other report of that kind is made. Two new specimens from a nursery labeled *C. tomentosa* are not like the older *C. tomentosa* planted here, but are more like *C. integerrima*, but larger.

It was noted above that two plants of *C. obscura* var. *cornifolia* Rehd. & Wils. coming from the same seed source were alike in every way, the chromosomes being similar in number and appearance. Several other groups of two or more specimens from the same collection of seeds from a species were growing in the Arboretum. In all these cases plants from the same seed sources were alike. The number was not large enough in

each case to be certain if this was always true for these species, but Cotoneasters in general were considered to come true from seeds.

In the behavior of the chromosomes definite groupings are suggested, and a few of these species are very close together. For instance, *C. francheti* and *C. schneideri* are similar, as are the two so closely related soongoricas. A note with one specimen of *C. francheti* in the cultivated group describes the fruit as orange-scarlet. Schneider collected an orange-scarlet-fruited specimen at Gotha. Perhaps this is where the name *C. schneideri* became attached to and substituted for *C. francheti* for the California plant, as *C. schneideri* does show a slightly more orange tint. At any rate, *C. francheti* is a tetraploid which shows a deep orange red as it is ripening, and only a slight variation could be the cause of the differences in both cases. *Cotoneaster wardii*, a related triploid, lacks the orange tint altogether. *Cotoneaster francheti* is a tetraploid, which explains to some extent the "splitters" that Turrill mentions in connection with the variety "*sterniana*" and which turns up in *C. schneideri*. Crosses with other species may help to produce the triploids found in cases like *C. wardii*, *C. nitens*, *C. divaricata*, and others.

REPRODUCTION IN COTONEASTER

Most of the Cotoneasters have long been known to breed true from seeds. This has been shown by the uniformity in the seedlings grown from the collections of Wilson and others, and frequent mention of the fact that certain species of *Cotoneaster* could be propagated by seeds. Saunders (60), in Refugium Botanicum, mentions that *C. buxifolia* comes true from seeds, and gives a list of Cotoneasters that may be propagated by seeds. Conrad Loddiges & Sons (41) describe *C. affinis* and *C. melanocarpa* as raised from seeds. According to Stapf's (66) description of *C. bullata* in the Botanical Magazine, 1909, it produces an abundant crop of seeds to increase the plant.

In the literature on *Cotoneaster* several cases of natural crosses have been reported. *Cotoneaster frigida* Lindl. is of interest in this respect. It has been mentioned as one of the parents in several instances.

Exell (17) collected seeds from a plant of *C. frigida* growing in close proximity to other species of *Cotoneaster* and planted them. Among the resulting seedlings there were six hybrids; the remaining plants were like *C. frigida*. *Cotoneaster watereri* Exell was considered an interesting hybrid between *C. frigida* Lindl. and *C. henryana* Rehd. & Wils. (*C. rugosa* Pritzel and Diels.). *Cotoneaster frigida* Lindl. and *C. pannosa* Franch. gave rise to *C. crispii* Exell. The others were not of horticultural interest.

A. A. Pettigrew (54) of Cardiff obtained seeds of a *C. frigida fructiluteo* plant from Stevenstone, Devonshire. This plant differed from the type in color of the fruit only, which was yellowish or creamy white instead of red. After several years of genetic experiments, on which the final report was not available, the author found red to be dominant, and

he believed that the individual plants of *C. frigida* were self-sterile and that they were fertilized by a red-fruited variety growing in the vicinity.

Conrad Loddiges & Sons (41), in describing *C. frigida*, mention that it should be budded on white thorn stock.

Another instance of the tendency of *C. frigida* to hybridize is the announcement, in Gardeners' Chronicle 132: 243, of *C. cornubia* — a hybrid between *C. frigida* and an unrecorded species — as a vigorous plant by Mr. Lionel de Rothschild in 1933. This received an award of merit.

Others report *C. frigida* as breeding true. A. T. Johnson (40) describes *C. frigida* as naturally a free and robust tree "so readily raised from seeds." He also mentions the distinct form *fructo-luteo*. Four seedlings of *C. frigida montana* grown from seed obtained by Donald Wyman from North Africa were alike.

On a note with a specimen from the Flora of Chumbi in the Arnold Arboretum Herbarium, mention is made of the fact that seedlings of *C. frigida* Lindl. are alike; also that seedlings of *C. aldenhamensis* are all alike but not so broad-leaved as those of *frigida*.

R. N. Parker, while collecting in Khadrula India Sikkum, Himalayas, at an altitude of 2700 meters, June 18, 1928, found in a thicket a specimen which he considered a cross (*C. acuminata* Lindl. and *C. rosea* Edgew.). There is a specimen of this in the Arnold Arboretum Herbarium. This has the habit of *C. acuminata* and the pink flowers of *C. rosea*. A plant of *C. rosea* was growing near by the thicket of *C. acuminata* where this hybrid plant was found.

Caution against raising plants from seeds comes from several sources, concerning both the *microphylla* and *salicifolia* groups. Of the probable hybridization in the several species allied to *C. microphylla*, *C. congesta* (Syn. *C. microphylla* var. *gracilis*), and *C. thymifolia* Arthur Osborn (51) writes, "It is best to propagate these distinct forms by cuttings or layers. They do not come true. At least that is our experience at Kew, though this may be due to cross pollination as all are growing in close proximity." W. J. Bean (3) made similar observations, as was noted earlier. The group of species, all natives of the upper and middle basin of the Yangtze River, in which are included *C. salicifolia* and its varieties, *C. glabrata*, *C. henryana*, and *C. rhytidophylla*, have also been reported (66) to hybridize easily. *Cotoneaster watereri* is supposed to have one parent in this group.

The instances of hybridization are few and limited to species or groups where few specific data are available. In an isolated population a species would be expected to breed true, but when numerous species are growing in close proximity variation would be expected. Some cases have been cited where a small number of offspring from the same seed source are alike when species overlap and hybridization could result. The most critical test, however, is the study of the progeny of species grown in a botanical garden where many species are grown in close proximity.

In the Arnold Arboretum most of the species are grown in close proximity, and the time of flowering is essentially the same in some species

and overlapping in others. There is ample opportunity for cross-pollination, since the bees at blossoming time are so abundant that it is difficult to work with the plants.

In order to determine whether most of the species breed true from seeds where there was so much chance of cross-pollination, seeds were collected from the following species, stratified, and grown in the greenhouse: *C. acuminata*, *C. acutifolia* var. *villosula*, *C. adpressa*, *C. adpressa hessei*, *C. adpressa* var. *praecox*, *C. ambigua*, *C. apiculata*, *C. bullata*, *C. bullata* f. *floribunda*, *C. dielsiana*, *C. divaricata*, *C. foveolata*, *C. frigida*, *C. horizontalis*, *C. integerrima*, *C. lindleyi*, *C. lucida*, *C. microphylla*, *C. moupinensis*, *C. nitens*, *C. obscura cornifolia*, *C. racemiflora* var. *desfontaini*, *C. racemiflora* var. *soongorica*, *C. racemiflora* var. *veitchii*, *C. rosea*, *C. simonsii*, *C. s.* var. *newryensis*, *C. tomentosa* and *C. wardii*.

In connection with this part of the work I wish to thank Dr. Karl Sax, who helped collect the seeds, and Mr. Lewis Lipp, Jeanette Renshaw and Dorothy Thorndyke for growing and caring for the seedlings. I thank George Graves, who grew additional seedlings from three of the same seed sources and furnished the data that are also included in the table (Table II). These include 25 seedlings of *C. apiculata*, 1000 of *C. dielsiana*, and 200 of *C. divaricata*.

TABLE II

APOMIXIS IN COTONEASTER

Species	Chromosome Number	Number of Seedlings	Number of Maternals	Number of Variants
C. acuminata	2 n	11	4	7
C. acutifolia var. *villosula*	4 n	14	12	2
C. adpressa	3 n	6	6	0
C. adpressa hessei	3 n	10	10	0
C. adpressa var. *praecox*	3 n	4	4	0
C. ambigua	3 n	50	50	0
C. apiculata	3 n	54	54	0
C. bullata	3 n	14	14	0
C. bullata f. *floribunda*	3 n	34	34	0
C. dielsiana	3 n	1673	1673	0
C. divaricata	3 n	200	200	0
C. frigida	2 n	2	0	2
C. horizontalis	3 n	5	5	0
C. integerrima	3 n	44	44	0
C. lindleyi	3 n	16	16	0
C. moupinensis	3 n	21	21	0
C. multiflora	4 n	57	57	0
C. nitens	3 n	26	26	0
C. obscura var. *cornifolia*	3 n	16	16	0
C. racemiflora var. *veitchii*	3 n	13	13	0
C. rosea	3 n	27	27	0
C. simonsii	3 n	384	381	3
C. wardii	3 n	36	35	1

The data for this work are given in Table II. In most instances the number of seedlings from each species was not large, but most of the offspring were like the seed parent; most were maternals.

Cotoneaster acuminata and *C. frigida* showed a tendency to hybridize. They showed considerable variation in their respective progeny. Both are diploids.

The large majority of the Cotoneasters breed true. Several others did show a small percentage of variants.

Among the triploids, three of those propagated threw a small percentage of variants (Table II). Of the 26 seedlings of *C. nitens*, three were different and varying among themselves; the others were alike. One of the thirty-six seedlings of *C. wardii* varied from the type. Of 384 seedlings of *C. simonsii* all were uniform, with three exceptions. As was also true of the aberrants in *C. nitens* and *C. wardii*, the three seedlings of *C. simonsii* were conspicuously different from the others of the same species. They were striking among an otherwise uniform population. They had broader leaves which were thicker and tomentose and flattened into a rosette.

This may indicate that although *C. nitens*, *C. simonsii*, and *C. wardii* reproduced apomictically, the egg is fertilized at least at times, and that they may be crossed with other species. They are probably facultative apomictic species, as *Malus sargenti* is among the apples.

On the triploid *C. tomentosa* (Ait.) Lindl. destyled ovaries developed in about the same proportion as on the controls on other branches of the same shrub. This was also true of the destyled ovaries of the triploids *C. dielsiana* Pritz., *C. nitens* Rehd. & Wils., *C. froebellii* — a plant from Vilmorin — and *C. zabeli* Schneid., but further work along this line would be necessary before settling this point on these grounds, except for a few species. Many species so treated gave negative results, but most of the negative results are not conclusive, either because not enough work was done, or because injury in the process might cause the fruit to drop (as happened most often the first year) or because no fruit was set on the controls at the same time.

Apomixis must be very general among the triploid Cotoneasters. Many species grown in the same vicinity are in bloom at the same time. The bees and other insects are attracted to them in such large numbers that cross-pollination should be the rule. Although the divisions in the pollen mother cells were very irregular in the triploids, and often with the loss of chromatin, there was an abundant production of fruit and a great uniformity among the progeny where they were tested. This seems to establish rather definitely the presence of apomixis in the triploids.

The tetraploids were more regular in the divisions in their pollen mother cells. Seedlings of only two tetraploids, *C. acutifolia* var. *villosula* and *C. multiflora*, were grown. Among fourteen seedlings of the former two variants appeared. All were uniform in *C. multiflora*. Abundant fruit set on the plant, which was in the midst of many other species.

There is no doubt about apomixis in the triploid Cotoneasters, and it

is possible that it may exist in some of the diploids and tetraploids. There is also some evidence that some of the triploids are facultative apomicts, since three produced a small percentage of variant seedlings. It is possible that variants in other triploid species might be found if larger numbers of progeny were grown or if the triploids were hand-pollinated with pollen from triploids.

The meagre evidence of facultative apomixis in *Cotoneaster* is supported by the breeding behavior of the closely related genus *Malus*. *Malus sargenti* is found in diploid, triploid, and tetraploid forms (K. Sax unpublished). When open pollinated all produce only maternal progeny, even though they are surrounded by other species. When artificially pollinated with pollen from other diploid species, the triploids and tetraploid *M. sargenti* forms do produce some sexual progeny, but seldom more than twenty per cent. In some cases only maternal types of progeny are produced, and in all cases these types are predominant. The mechanism of this facultative apomixis is unknown. A few triploid species of *Malus* do produce an occasional variant when open pollinated, even though the great majority of the progeny are maternals. It is possible that the same type of apomixis is present in *Cotoneaster*.

DISTRIBUTION AND RELATIONSHIPS

The geographical distribution of *Cotoneaster* in relation to the 2 n, 3 n, and 4 n chromosome numbers may offer suggestions as to the origin of some of the species. Eight of the species studied are diploids. There may be other diploids among those in which the chromosome number has not been determined. The diploids *C. frigida*, *C. microphylla*, and *C. acuminata* are found in the Himalayas; *C. conspicua* in Tibet; *C. glabrata* and *C. henryana* in the Yangtze basin in western and central China; *C. dammeri* in West Hupeh in central China; and only one, *C. acutifolia* Turcz., in North China and Mongolia.

The diploids have a limited geographical distribution, and fifty per cent of them are found in Zone 7 (Rehder); only one, *C. acutifolia* Turcz., inhabits Zone 4. Wilson (75) comments that *C. acutifolia* Turcz. was originally described from Chinese Mongolia, that it was introduced by Dr. Bretschneider from mountains near Peking, and that the typical form is absent from central and western China, but varieties are found growing in these regions.

There were a number of instances in which specimens were labeled *C. acutifolia* or a variety thereof. Some of these have been considered as natural variations. Some relatives of *C. acutifolia* Turcz. have been recognized, but the situation was complex, and much has been left to be settled in the future.

A variety, *C. acutifolia* var. *villosula* Rehd. & Wils., was recognized as a near relative. A study of the chromosome number proved it to be a tetraploid form. It is a hardy shrub occupying Zone 5 in central and western China. It grows in thickets in West Hupeh, West Szechuan, and

in the Shensi mountains, the latter bordering on the habitat of *C. acutifolia* Turcz. It may have originated through the doubling of the chromosome number of *C. acutifolia* under circumstances in the past conducive to the disturbance of the chromosome balance. Two specimens labeled *Cotoneaster* sp. grown in the Arnold Arboretum from seed collected by Dr. Rock in the Tao River Basin in western China were triploids.

A large number of species which are considered as belonging to the "acutifolia group" are triploids or aneuploids with approximately the 3 n number. Included in this category are *C. ambigua* Rehd. & Wils., which the authors considered closely allied to *C. acutifolia* Turcz., and *C. obscura* Rehd. & Wils., which they believed resembled *C. acuminata* which grows in the Himalayas in India. They thought *C. obscura* also resembled *C. foveolata* Rehd. & Wils. of West Hupeh, which seems more probable, although there may have been earlier connections with the *acuminata* ancestors. *Cotoneaster foveolata* Rehd. & Wils. in turn closely resembles *C. moupinensis* Franch., common in the thickets of West Szechuan. These were black-fruited. *Cotoneaster bullata* Bois. and its varieties are red-fruited, and when not in fruit were mistaken for *C. moupinensis*. Further comments show close external resemblance. *Cotoneaster bullata* Bois., according to Wilson, is a relatively rare plant but is widely scattered along the edge of the zone occupied by *C. moupinensis* in West Szechuan.

At first Rehder and Wilson considered *C. tenuipes* Rehd. & Wils. as nearly related to *C. racemiflora* Koch (which is on the other side of the mountains), but they lacked the flowers. Later Rehder placed it near *C. acutifolia* Turcz., which seems more probable, as these forms are all found in West China.

These triploids that resemble *C. acutifolia* Turcz. may have come from the diploid *C. acutifolia* and the tetraploid *C. villosula*. There is also the possibility of intercrossing of *C. villosula* and its descendants with other diploids of the region, as is obvious from the geographical locations and the fact that *C. acutifolia* var. *villosula* is a facultative apomict.

Cotoneaster acutifolia Turcz. may also have contributed some of its characteristics to the flora of the North. *Cotoneaster lucida* Schlecht. was once named *C. acutifolia* Lindl. It is not easily confused with *C. acutifolia* Turcz. It has dark green leaves which are very glossy and lustrous. It has also been found to be a triploid. It grows in the Altai mountains in Mongolia in Zone 4 (Rehder), in thickets at 2000–3000 m., having a limited distribution. This is probably related to *C. acutifolia* Turcz. and may have another relative in *C. melanocarpa* Lodd.

Cotoneaster melanocarpa Lodd. is a tetraploid species which ranges from northern and eastern Europe across Siberia to central and northeast Asia. It is probable that it is another tetraploid form from *C. acutifolia* Turcz. (or even *C. acuminata*, which I doubt) which, having less competition to the north as well as the necessary vigor and better adaptability, has occupied more space than most Cotoneasters. It inhabits Zone 4.

Varietal forms of *C. melanocarpa* Lodd. occupy more restricted areas.

The variety *C. melanocarpa* var. *commixta* Schneid. is a 4 n species and *C. melanocarpa* var. *laxiflora* (Lindl.) Schneid. is a 3 n species from central Asia. It may have been a back cross of *C. melanocarpa* with *C. acutifolia* or a cross with *C. acutifolia* var. *villosula.*

Other diploids have contributed variation to the flora around them. *Cotoneaster acuminata* Lindl. is a diploid found in Zone 5 in the Himalayas and on the side away from China. According to Wilson (75) *C. acuminata* Pritzel in Bot. Jahrb. 29: 385. 1900 (pro parte, non Lindley) is under *C. acutifolia* var. *villosula* as a synonym. There are different as to chromosome number and they are geographically separated.

Although they are distinct species, there is some resemblance and a fairly close relationship taxonomically between *C. acutifolia* Turcz. and *C. acuminata.* They may have some common or similar ancestry in the past; at present there are very definite geographical barriers between the species.

Cotoncaster frigida Lindl., a diploid, grows in the Himalayas and is cultivated in Zone 7. Rehder (56) considers *C. affinis* and its variety *C. affinis* var. *bacillaris*, a tetraploid cultivated from Zone 7 (?) to be closely related to *C. frigida.* Bean (3), in his "Trees and Shrubs," remarks that *C. affinis* var. *bacillaris* and *C. frigida* are connected by one or two intermediates. In 1899, W. J. Bean writes in Vol. 55 of The Garden that *C. affinis* is between *C. bacillaris* and *C. frigida.* The tetraploid *C. affinis* var. *bacillaris* may have been formed by a cross between two species, one of which was *C. frigida*, or by the doubling of the chromosome number of *C. frigida.*

Cotoneaster lindleyi, a triploid, also shows affinity for this group, especially *C. racemiflora.* It is an inhabitant of the Himalayas, and is cultivated in Zone 6 (?).

Cotoneaster racemiflora (Desf.) K. Koch is considered by Rehder a very variable species. It is a triploid which ranges in Zone 4 from southern Europe, North Africa, and western Asia to the Himalayas and Turkestan. It has several varieties, var. *desfontaini* (Reg.) Zab. being the typical one, and it is a triploid. It is not found in China, but some of its varieties are found there and are more limited in distribution. *Cotoneaster racemiflora* var. *soongorica* (Reg. & Herd.) Schneid. inhabits West China, Zone 3, and *C. racemiflora* var. *veitchii* central China. These are triploids.

If the species in China are closely related to the species to the west, then a common ancestor must have given rise to those on both sides of the mountains. Its wide range makes *C. racemiflora* look like an older species. It may have come from *C. frigida*, at least as one of the parents, in which there was a doubling of the chromosomes, as is probable in *C. affinis* var. *bacillaris*, or it may have come from a cross of *C. frigida* with *C. acuminata* or an unknown or extinct species. It is apparent that there is a decided difference between the Chinese *racemiflora* species and the typical form.

That the *C. racemiflora* triploids which were grown in close proximity with other Cotoneasters breed true shows that apomixis is fairly common.

The seed set is very good. The wide range of these triploid apomicts shows ability to adapt to a variety of locations. *Cotoneaster rosea* shows resemblances to *C. racemiflora*. It may show both *C. acuminata* and *C. frigida* traits. It is a triploid.

Cotoneaster simonsii, first collected in the Khasia Mts. in northern India, shows some resemblance to *C. acuminata* and to *C. rotundifolia*. There is a possibility that in the past it had some common ancestry with the francheti group — to which it is often likened.

Several of the most attractive species of *Cotoneaster* which show various degrees of similarity inhabit West and Central China. They differ from the *acutifolia* group. Among these are *C. francheti*, a tetraploid, and the triploids *C. dielsiana*, *C. dielsiana* var. *elegans*, *C. divaricata*, and *C. nitens*. *Cotoneaster wardii*, a triploid facultative apomict inhabiting Tibet, is very closely related. *Cotoneaster dielsiana* is an apomict. *Cotoneaster zabeli*, which inhabits central China, appears to have some similar traits. It and its variety are both triploids.

The origin of this group is not clear. They are all related to the tetraploid *C. francheti* Bois. The diploid *C. dammeri* grows in central China, *C. conspicua* in W. China. There are also possibilities of having earlier species mixed with ancestors of species from the southern Himalayan groups. *Cotoneaster microphylla* extends into Yunnan. Further study of the *francheti* group is necessary in order to determine its origin.

The *salicifolia*-like group of plants from the Yangtze Basin have been a problem to the systematist. *Cotoneaster salicifolia* Franch., its varieties *floccosa* (Pritz.) Rehd. & Wils. and *rugosa* Rehd. & Wils., *C. rhytidophylla* Rehd. & Wils., *C. glabrata* Rehd. & Wils., and *C. henryana* (Schneid.) Rehd. & Wils., are all evergreen or half evergreen species with prominently veined, elliptic oblong to ovate lanceolate leaves. They have attractive flowers and fruit.

Exell (17) remarks, "I am following the conclusions of Dr. Stapf (Bot. Mag. *t. 8999*) that *C. henryana* Rehd. & Wils. and the earlier *C. rugosa* Pritz. ex Diels are synonymous." These plants do resemble each other closely, but Rehder & Wilson (56) recognized some differences, and the study of the chromosome numbers indicates that they were correct. *Cotoneaster glabrata* and *C. henryana* are diploid species (Rehder Zone 7 ?). *Cotoneaster salicifolia* comes from Zone 6 (?). Its chromosome numbers have not been determined with certainty. Its variety *C. salicifolia* var. *rugosa* is a triploid from Zone 5.

It may be noted from the zones in which these species are found that they are fairly tender plants. Except *C. rhytidophylla* Rehd. & Wils. they are all growing in the Arnold Arboretum (in fairly protected areas) in Zone 4.

It is not surprising that Thomas (72) remarks, "If these plants are raised from seeds variation results." There are some diploids, *C. glabrata* and *C. henryana*, and some triploids. There may be facultative apomicts in some of this group.

Included by Rehder as a nearly related species is *C. glaucophylla*

Franch. inhabiting West China (Zone 7) which is also a triploid. He calls attention to some resemblance to *C. zabeli*. *Cotoneaster zabeli* is a triploid from central China. A variety, *C. zabeli* var. *miniata* Rehd. & Wils., is a triploid from central China.

The *microphylla* group, mostly prostrate plants, inhabits the Himalayas. E. H. Wilson (75) remarks that it is not seen in China, although it has been reported from Yunnan. These plants are reported to show variation in their seedlings. *C. microphylla* is a diploid. There are several *microphylla* varieties with closely related species, as *C. congesta* Bak. (Himalayas). Rehder mentions *C. conspicua* Marquand, a diploid, as a closely related species. It inhabits West China and Tibet.

It may be noted from the foregoing that the triploids vary more as to range and habitat. Some of them are as limited as the diploids, being reported from only one vicinity. Nineteen out of about forty triploids are reported from West China, four from the Himalayas, and six from Central and West China. Four more are described from Central China, two from North China, and one, *C. multiflora granatensis*, from Spain. All of these show a narrow range.

There are a few more widely ranging triploid species. *Cotoneaster integerrima* Med., an early recognized *Cotoneaster*, is a triploid which is common to Zone 5 in Europe, in the western Himalayas, and in northern Asia to the Altai Mountains in Mongolia. It has been reported from southeast Tibet and Shantung, far from any others that have been reported. Rehder collected it for the Arnold Arboretum in the Savoyan Alps in France, and Anderson collected it in the mountains in Bulgaria. Rehder considers *C. uniflora* Bge., growing in the Altai Mountains, as a closely related species, but comments that it may be only a variety of *C. integerrima*. *Cotoneaster sylvestris* of central China is also mentioned as a closely related species. *Cotoneaster zabeli* of western China shows some characteristics of *C. integerrima*.

Cotoneaster tomentosa (Ait.) Lindl. is somewhat more limited in its distribution. It grows in northern and eastern Europe and western Asia. It has been reported from Kansu. It is considered related to *C. integerrima*, but it is larger and more intense in every detail. It is a vigorous apomictic triploid. *Cotoneaster tomentosa* leaves are more like those of the *affinis* group but heavier and more tomentose; these species differ in fruit and inflorescence.

Another widely distributed triploid, *C. racemiflora*, is found growing from North Africa throughout southern Europe and western Asia to the Himalayas and Turkestan. It is reported at Tomsk in Siberia. J. F. Rock remarks that the typical *C. racemiflora* (Desf.) K. Koch is not found in China, but well-marked varieties are found in Hupeh and Szechuan. The McClaren collectors found *C. racemiflora* var. *veitchii* in the Purple Mountains near Nanking. The variety *C. racemiflora* var. *soongorica* has been collected in West China, Shantung, and Shansi.

Of the large number of triploids only two, *C. glaucophylla* and *C. wardii*, are found in Zone 7 (both questioned); six are in Zone 6, and *C. racemi-*

flora var. *soongorica* is in Zone 3. The remaining triploids in which the chromosome numbers were determined were either varieties or unknown species.

The tetraploids, which are few in number, also vary in the breadth of their distribution. *Cotoneaster acutifolia* var. *villosula* is a tetraploid from central and western China in Zone 4. *Cotoneaster affinis* var. *bacillaris* inhabits Nepal (Zone 7), *C. francheti* western China (Zone 6 ?). *Cotoneaster melanocarpa* ranges in Zone 4 from northern and eastern Europe and the Caucasus to central Asia (having been reported from Tomsk), from Turkestan through Siberia to northeast Asia in Mongolia, Manchuria, Chili and Kansu. The variety *C. melanocarpa* var. *commixta* has a more limited range. *Cotoneaster multiflora* is found in West China. *Cotoneaster melanocarpa* has the widest range of the Cotoneasters except the triploid *C. racemiflora*.

Some of the polyploids show a tendency to adapt themselves over a wider range geographically. The diploids are limited in their range. There is also a slight tendency for the diploids to be more limited zonally, about half being in Zone 7.

All European species so far studied are polyploid. They probably originate from the Himalayan species. No diploids are found in Europe, and all European species show resemblances to those of central and northern Asia. *Cotoneaster multiflora* var. *granatensis* from Spain is supposed to be related to *C. multiflora* from western China. It might, however, be related to *C. racemiflora*, which is not so far apart from *C. multiflora* in distinguishing characteristics. Its leaf pubescence is characteristic of *C. racemiflora*, being one of the characters separating the two species.

When the chromosome number and the tendency to be evergreen were considered at the time of leaf drop there was found to be a slight tendency on the part of the 2 n species to be more evergreen and therefore more subtropical. There were deciduous diploids, *C. acutifolia* and *C. acuminata*. There were many polyploid evergreens. Some of the plants, both diploid and polyploid, were partially evergreen.

VARIATION AND EVOLUTION

Cotoneaster has long been recognized as a taxonomically difficult genus. Wilson (75) in discussing the similarities of the black-fruited Cotoneasters from China wrote "with *C. acutifolia* Turcz. at one end of the chain and *moupinensis* Franchet at the other, it is almost possible with the material before us to connect the series." As in *Hieracium*, *Crataegus* and *Rubus*, the species and varieties are often separated by minute, but constant differences.

Hybridization is still a prominent factor in the variation and evolution of the Cotoneasters. There is clear evidence of hybridization of the diploid species, both in nature and under cultivation. There is some indica-

tion of crossing between a few of the tetraploids. It is also probable that many, if not most, of the triploids were derived from crosses between diploids and tetraploids. Even some of the apomictic triploids may occasionally hybridize with diploids, as is known to be the case in *Malus*.

Although the great majority of the species of *Cotoneaster* are apomictic triploids, there are some variants among the progeny of some species. Such variation could be caused by occasional sexual reproduction, or it could be the result of internal segregation if the progeny are from unreduced egg cells, as Haskell (34) has suggested for apomictic species of *Rubus*. The meiotic irregularity and loss or non-disjunction of chromosomes could also lead to variant aneuploids, as has been suggested by Stebbins (68). There is some evidence of aneuploidy in a few Cotoneasters, although exact chromosome counts were not possible.

In the triploids the meiotic divisions are irregular, as may be expected, but some species are more irregular than others, with bridges found at anaphase. Although the division process is typical for each species or variety, there is much variation between the speices, and due to various degrees of adherence of the homologues, the exact chromosome number is sometimes uncertain. Some of the speices may be aneuploid with slight differences in chromosome number; some of the chromosomes may be lacking, but this has not been established.

Perhaps these more irregular triploids are from crosses between distantly related diploids and tetraploids which differ in chromosome structure and result in inversion bridges in the triploid hybrids. The more regular triploids may be autopolyploids between closely related forms. At any rate, the triploids do seem to fall into several rather distinct groups in respect to meiotic behavior.

Polyploidy within the species would also account for some variation since it is known that induced tetraploids are often of a stiffer habit and have larger and more deeply colored flowers than their diploid ancestors. It is just this type of variation that differentiates many of the species and varieties of *Cotoneaster*.

The variation produced by hybridization and polyploidy is "fixed" by apomixis. Although, as Müntzing and others have found, apomixis is not confined to polyploids, it does permit cytologically and genetically heterozygous species to be perpetuated. Slight variations can be maintained in "Clonal Species," a term proposed by Darlington (10).

Apomixis in polyploids permits the constant reproduction of a hybrid which would normally be sterile and would have little survival value. Yet it is known that many artificially produced triploids which must be propagated by grafts or cuttings are superior to either the diploid or tetraploid parent in vigor and in horticultural value (K. Sax unpublished). The fact that most of the species of *Cotoneaster* are apomictic triploids shows that they have high survival values and can be easily propagated.

The polyploid species of *Cotoneaster* do have a wider range of distribution than the diploids. The diploids are largely confined to the Himalayas, West and Central China, while some of the triploids and tetraploids are widely distributed. The triploids *C. racemiflora*, *C. integerrima*, and *C.*

tomentosa have occupied a wide territory. *Cotoneaster lucida*, although limited in distribution, has adapted itself to a colder zone. The tetraploid *C. melanocarpa* has spread over large areas from northern and eastern Europe through Siberia and Manchuria. These widely distributed species are polyploid apomicts.

Excessive uniformity brought about by apomixis might be a handicap, even though under original conditions the triploid or hybrid apomictic species may have definite advantages and greater adaptability. As Stebbins (68) has suggested, the uniformity imposed by apomixis would be a handicap in a changing environment, and the lack of variation would be a block to further evolution.

In *Cotoneaster*, however, there is occasional variation in the progeny of apomictic species. These species still have some plasticity to meet a changing environment, either through occasional sexual progeny, internal segregation, or chromosome irregularity. Thus they have the ability to perpetuate an unbalanced cytological and genetic complex of adaptive value and yet have the capacity to produce variants to meet new environmental conditions.

Polyploidy and hybridization provide most of the variation in *Cotoneaster*. Often the differences are slight, yet they are fixed by apomixis, providing distinct variants which reproduce true to type. Some of these may have a wide distribution. It is this complex of variation due to polyploidy and hybridization, combined with apomixis, that makes the genus *Cotoneaster* a difficult one for the taxonomist. For the horticulturist apomixis is an advantage, since most of the ornamental species and varieties breed true from seed.

SUMMARY

The chromosome numbers were determined in forty-one species and eighteen varieties of *Cotoneaster*. Of these Cotoneasters eight taxa were diploid, forty-three triploid, six tetraploid, and two polyploids could not be determined. Some aneuploidy may be present, as several triploids seem to vary.

Progeny from twenty-three species show that two diploids reproduced sexually. The rest reproduced apomictically, an occasional variant appearing among three of the nineteen triploids: *C. nitens*, *C. simonsii*, and *C. wardii*. One tetraploid was a facultative apomict.

The diploids are limited in their geographical distribution, as are most of the triploids and tetraploids. Among the triploids three species, *C. integerrima*, *C. racemiflora*, and *C. tomentosa*, show wide distribution. One tetraploid, *C. melanocarpa*, is found over wide areas. The diploids showed a slight tendency toward zonal, as well as geographical limitation.

Apomixis stabilizes a species, but the genus *Cotoneaster* is given flexibility through sexual reproduction and through facultative apomixis. There are probably some obligate apomicts, i.e., *C. dielsiana*.

Apomixis and polyploidy are responsible for the taxonomic complexity of the genus *Cotoneaster*.

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THE DIRECTOR'S REPORT ON THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1954

The fiscal year of 1953–54 was a momentous one for the Arnold Arboretum, marking as it did the solution of long-standing problems of space, housing and care of collections which have for over a decade hindered the work of the Arnold Arboretum.

On January 19, 1953, the President and Fellows of Harvard College (the trustee of the Arnold Arboretum), in a detailed and careful vote, stated that "In the exercise of its duties as trustee of the endowment funds held in trust for the purposes of the Arnold Arboretum, the Corporation determines that it is in the best interests of the Arboretum and will promote the purposes of its endowment to remove to a central building in Cambridge the main body of the library and herbarium of the Arboretum related to research, and to retain in Jamaica Plain such books and specimens as may be required to provide there a working library and herbarium." This proposal had long been advocated as a solution to the problems of the Arboretum which previous directors have stated in their annual reports. (See Annual Reports 1936, 1938, 1940, 1941, 1942 and following.) The Administration Building in the Arboretum had become overcrowded. Floor space was no longer available for the addition of steel cases, and as temporary expedients, display cases and cardboard herbarium boxes were used to store approximately 20% of the mounted herbarium and all of the material awaiting determination and mounting. The library was equally crowded to the point where it was becoming difficult to care for the valuable books properly. This latter condition had been alleviated by transferring, for use and storage, many of the Arboretum books to the Harvard Forest and to Cambridge. However, even with these measures, additional shelf space could not be found in the Administration Building. Working space for staff members had become restricted by the growth of the collections and the library. To solve these and other problems, the Corporation vote was welcomed by a majority of the staff of the Arboretum.

The vote of the Harvard Corporation called for the appointment of an Arnold Professor, a post unoccupied since the retirement in 1946 of Dr. E. D. Merrill. In October the Corporation, with the approval of the Board of Overseers, appointed Richard Alden Howard as Arnold Professor and Director of the Arboretum. Dr. Howard was also appointed Professor of Dendrology within Harvard College. All appointments were effective February 1, 1954.

The Harvard Corporation had voted that a portion of the herbarium and library was to be moved to a new building in Cambridge known as the Harvard University Herbarium Building. One million dollars was assigned from unrestricted funds of the University for the construction and equipping of this building. The Arboretum collections and library would thereby receive adequate housing and the staff working equipment at no

capital cost to the Arnold Arboretum endowment. Construction of the building was completed in February 1954.

The Arnold Professor, by vote of the Corporation, was to implement the move. Serious consideration was then given by the director and the staff of the Arboretum to the selection of books and herbarium specimens to be retained in Jamaica Plain. When tentative plans were formulated, Dr. Howard, in accordance with the vote of the Corporation, consulted with Dr. William J. Robbins, Director of the New York Botanical Garden, regarding what specimens were to be left in Jamaica Plain as a working herbarium. He also consulted with Dr. Keyes Metcalf, Director of the Harvard University Libraries, regarding what books were to be retained in Jamaica Plain. Each of these conferences produced a final plan which determined the nature of the Arboretum's collections of specimens and books in each of the two locations. Dr. Robbins and Dr. Howard determined that the vote of the Harvard Corporation could be best implemented by establishing in Jamaica Plain a working herbarium devoted to the study and advancement of knowledge of horticultural plants. To that end they made seven recommendations as follows:

1. That all cultivated specimens in the herbarium of the Arnold Arboretum representing taxa now under cultivation in the Arboretum and elsewhere be retained in Jamaica Plain.
2. That sufficient additional specimens of taxa related to a given cultivated group be retained to insure working control of that group.
3. That spontaneous or native specimens be used to supplement poorly represented cultivated taxa.
4. That representative specimens of all taxa of certain major cultivated groups be retained. For example, it is proposed to have in Jamaica Plain all material of the difficult genus *Crataegus*, and to have representatives of all taxa of the Conifers, *Rosa*, *Rhododendron*, *Cotoneaster*, *Quercus*, *Syringa*, *Viburnum*, *Lonicera*, *Fraxinus* and *Ulmus*.
5. That additional specimens be returned to the herbarium at Jamaica Plain as their need becomes known; i.e., new introductions, new cultigens, or additional material found necessary for determination.
6. That this herbarium be maintained as an active herbarium and that additional cultivated material, e.g. herbaceous specimens, be added in future years to make the herbarium at Jamaica Plain a complete working herbarium for determination and study of all groups of cultivated plants.
7. That all type specimens of cultivated taxa remain in the Jamaica Plain herbarium and be clearly marked and properly housed.

The specimens to be retained in Jamaica Plain number approximately 100,000 specimens and are housed in 96 steel herbarium cases, creating in itself one of the outstanding horticultural herbaria of the world.

A similar set of proposals was worked out by Dr. Metcalf and Dr. Howard regarding the library books to be retained in Jamaica Plain. Again, in accordance with the vote of the Harvard Corporation and for the best interests of the Arboretum, Dr. Metcalf and Professor Howard

recommended the establishment of a working library devoted to the study and advancement of knowledge of horticultural plants. To that end they recommended to the Corporation the following proposals:

1. That the library in Jamaica Plain retain a complete set of all publications of the Arnold Arboretum; i.e., the serial publications Arnoldia, the Journal of the Arnold Arboretum and Sargentia, as well as the complete sets of publications by staff members. All Sargent, Wilson and Rehder publications will be kept in Jamaica Plain.
2. That reference books for horticultural study and research are to be retained. These will include basic textbooks, floras, garden dictionaries, horticultural encyclopedias, and all books which normally fall in the library classification of horticulture, botanic gardens, etc.
3. That a selection of books on dendrology, ecology, physiology, pathology, economic botany, entomology, biography and natural history, as well as books on color will remain in Jamaica Plain.
4. To coordinate the interests of the herbarium with those of the library, there will be in Jamaica Plain all books dealing with roses, rhododendrons, lilacs, and similar groups, as well as monographs of *Crataegus*, *Quercus*, and the Conifers, and other horticultural books and monographs which will strengthen the value of the horticultural herbarium.
5. Additional periodicals of particular value to horticultural research and reference, such as Curtis's Botanical Magazine, Horticulture, Gartenschönheit, La Belgique Horticole, Revue Horticole, Gardener's Chronicle, Journal Royal Horticultural Society, etc., will be retained.
6. Folio volumes useful to horticulture are to be left in Jamaica Plain.
7. The large collection of Wilson photographs, photos of botanical gardens, cultivated plants, etc., are to be considered library material and retained in Jamaica Plain. The Rehder card catalogue considered essential in the use of the cultivated plants in the herbarium also will remain in Jamaica Plain.
8. All books, manuscripts and comparable reference material are to be catalogued on cards available in Jamaica Plain, and suitable designation of the location of these books is to be made in the Union Catalogue at Widener Library.
9. Additional books or similar reference material that may be found necessary in Jamaica Plain will be returned for permanent deposit in the library of the Administration Building.
10. The library of the Arnold Arboretum in Jamaica Plain and in Cambridge is to be considered in the future, as it is now, a reference and non-circulating library.

These proposals for a library dealing with cultivated plants consider approximately 7000 volumes of the total Arboretum library, including 1800 periodicals and 100 folio volumes.

Further consideration was taken by the staff as to the proper housing and location of books and specimens in the Administration Building in Jamaica Plain. Tentative plans were drawn for a redesigning of the interior of the Administration Building for horticultural activities. It was

proposed to house the library, offices, and herbarium on the first floor of the building. With the additional space available, a lecture-demonstration room will be possible, also on the first floor. Adequate storage and expansion for both the library and herbarium and sufficient working space for the staff is again possible in the building.

After all aspects of the proposals and plans were reviewed by the staff of the Arboretum, Dr. Howard submitted a report to the Corporation stating his recommendations for the implementation of the Corporation vote of January 19, 1953. The Corporation at their meeting on May 17, 1954, invited Dr. Howard to appear and to describe the procedures followed in preparing his recommendations. Later in the same meeting, the Corporation voted that the several recommendations presented by the Arnold Professor and Director of the Arnold Arboretum were in accordance with the statement of policy in the resolution of the Corporation of January 19th. The Corporation accepted Dr. Howard's recommendations and authorized him to proceed in accordance with those recommendations to carry out plans for the removal from the Administration Building in Jamaica Plain the herbarium specimens and books selected for location in the University Herbarium in Cambridge.

With this authorization the move began on June 7th and was in progress at the end of the fiscal year. The herbarium staff proceeded to draw out the herbarium specimens to be retained in the cultivated herbarium and to arrange these in the steel cases on the first floor of the Administration Building. The librarian, with additional assistance, selected the books to be retained in Jamaica Plain and these were arranged temporarily in the library reading room on the second floor until their permanent quarters on the first floor have been completed. The shifting of both the herbarium and the library was coordinated in such a way that there was no interruption of horticultural work or of service determinations. By July 1st the herbarium of cultivated plants in the Administration Building was completely organized and in use. Casey and Hayes Company, movers, were charged with the task of moving the herbarium cases with the specimens intact to the new building. The library to be moved was so organized that the books were taken from shelves in Jamaica Plain and placed on previously designated shelves in the new library in such a fashion that the books were always in order. Only the highest praise can be suggested for care afforded both the books and the specimens in the course of the move. The Art Metal Company, which originally supplied the steel herbarium cases of the Arnold Arboretum, was responsible for disassembling the cases in Jamaica Plain and reassembling them in Cambridge. That work is in progress. All cases are to be checked and new felts applied where necessary to assure that the old cases in their new location will be bug-proof. A large number of herbarium specimens had to be transported from Jamaica Plain to Cambridge in the cardboard herbarium boxes which had been their location for a decade. Eventually these specimens will be arranged in proper sequence in the regular herbarium and all will be stored in steel cases. The appropriation by the Corporation from University

funds allowed the purchase of 430 additional steel herbarium cases. The majority of these will be used to house the Arboretum's collections. Within the next year the Arboretum specimens for the first time in many years will all be housed properly in steel cases.

The Director can only speak with praise of the yeoman's service rendered by the Curator, the Librarian and many members of the staff who worked so hard to implement this move. A major goal in the care of the Arboretum's collections is near attainment, and while many months of hard work remain, the best interests of the Arnold Arboretum have been fully considered in the activities of the past year involving the move.

Horticulture:

Living collections of plants such as those that comprise the Arboretum's collection require constant care. The excellent condition of the grounds throughout the year and the outstanding floral display of the spring of 1954 are indicative of the activities of the horticultural staff.

During the past year approximately 150 species and varieties of new plants were added to the collections in Jamaica Plain. Many others were received either as seeds or living plants. These have been grown or propagated and are now being tested in our nurseries. A total of 152 shipments including 790 species and varieties was received. Most of these came from arboreta, gardens and nurseries in the United States and Japan, but shipments originated also in eight other countries. Over 50 species and varieties of Post Entry Quarantine plants were released by the U.S. Department of Agriculture, Bureau of Plant Quarantine, and these are being propagated for distribution as they show ornamental value. The propagation department prepared 7396 plants for our collections or for exchange or other distribution. These plants were propagated: cuttings, 4164; grafts, 2717; seeds, 485, and layering, 30. During the past year 144 shipments of plant materials were sent to cooperating institutions in eleven countries. Five small tree species, either new or extremely rare in America, were propagated and distributed to 24 cooperating nurseries which requested materials from a previously circulated list. Nearly 1000 individual plants were distributed to "Friends of the Arboretum" throughout the year. Several large yews and other shrubs were given to the Department of Buildings and Grounds of Harvard University for planting about the University Herbarium Building and other college buildings.

Pruning, fertilizing, spraying and planting operations continue throughout most of the year at the Arboretum. In the past year the base of Hemlock Hill was cleaned of weed growth, opening an area for a new hemlock planting at some future date. Many weed plants were pulled from the azalea bank on South Street and in the Kalmia collection on Hemlock Hill. The Taxus collection and the large pines along Walter Street were given a much-needed thinning, as were the azaleas on Bussey Hill.

Thirty-one cords of manure were spread on collections needing fertilizer.

These collections included the plantings of *Carpinus*, *Juniperus*, *Chamaecyparis*, *Viburnum*, *Rhododendron* and some of the *Rhododendron obtusum kaempferi* in the woods near the ponds. The Rhododendron collection had a splendid display of bloom this year as a result of repeated fertilizer applications of past years. Castor pumice has been used extensively on these plantings. Summer watering has also improved the condition of these plants.

The bank along the railroad tracks was sown to grass in the fall and several groups of conspicuous blooming trees were planted there this spring. Within a few years we hope to develop this bank into a colorful display, primarily for the benefit of the commuters on the Dedham branch of the New York, New Haven and Hartford Railroad.

A new "Bean" 400-gallon hydraulic sprayer was purchased to be drawn by tractor. It has become increasingly evident that control of all insects and diseases in the Arboretum merely by mist spraying is impossible. Both mist and hydraulic spraying are used now with better coverage and control that was formerly possible. Spray equipment was used on 24 different days last year. Particular attention to sprays and techniques of spraying for use in arboreta and parks is being given under the direction of the Superintendent and his staff. Fireblight, which in the past few years has become a serious threat to the large crab apple collection, was apparently held in check this year by the experimental use of "Agrimycin," one of the new antibiotics. A supply of this material for testing was donated by the Chas. Pfizer Company of New York. Weed control by the use of chemicals on a rigid spraying schedule has made poison ivy much less evident this year than before. The plant still grows in the Arboretum, however.

The locations of all cultivated plants on the 265 acres of the Arboretum are recorded on 74 standard maps scaled at 20 feet to the inch and 34 additional enlargements covering the congested areas. Of these 108 maps, approximately one-third are carefully field-checked each year. The condition of the plant is noted so that it can be propagated, fertilized, sprayed, labeled or given any treatment deemed necessary. Each year it is necessary to replace from 1500 to 2000 display labels which have disappeared or are illegible. At the same time identifications are checked and kept up to date with current taxonomic revisions. Last spring all the lilac collection was checked during the flowering period. A few plants were discarded as not being true to color and the remainder are now considered correct according to the most recent survey of "Lilacs for America," published by the Lilac Survey Committee of the American Association of Botanical Gardens and Arboretums. To further enhance the value of this collection to the public, selected plants were labeled "best of the variety" during the flowering season.

The collection of photographs owned by the Arboretum is used constantly for reference by the staff. Prints of these photographs are used by the staff to illustrate articles for publication. Photographs from our

files were also used in several national garden magazines and in newspapers. In recent years a collection of 35 mm. Kodachrome slides and 5 × 7 Ektachromes has been built up. These are used to illustrate lectures and publications. This collection is increased yearly and its use grows. Many of the photographs in these collections are made in private gardens in the vicinity of Greater Boston. The splendid cooperation of home owners who have unusual or interesting plant materials being used to advantage and who have given Arboretum staff members permission to photograph them is greatly appreciated. Within the past year postcards have been made from some of the kodachromes taken in the Arboretum. These are on sale at the Administration Building and in Boston and have proven popular among visitors.

The staff of the Arboretum remains active in the field of plant propagation. The use and effect of various plastic films in vegetative propagation is receiving considerable attention. Species of *Magnolia*, *Ilex* and *Acer* which are normally difficult to root are being tried under polyethylene plastic. The effect of polyethylene plastic as a tie material over graft unions is being tested on species of *Picea*, *Pinus* and *Abies*. A polyethylene grafting case has been used in propagation of species of *Ulmus*, *Quercus* and *Betula*. The same plastic film is being tested as a means of preventing the drying of seeds during stratification.

Acer griseum, one of the unusual maples in the Arboretum collection, is being tested for the effect of different root stocks on compatibility. Various concentrations of hormones on the rooting of *Rhododendron* species and varieties is being undertaken. Artificial pretreatment of seeds requiring a high temperature period followed by a low temperature is being applied to species of *Viburnum*, *Cotoneaster* and *Acer*. Reports will be published on the results of these experimental projects as the work progresses.

The horticultural staff has also demonstrated the popularity of the Arboretum collections through a program of adult education. Informal classes were held in the greenhouses, and the Fall and Spring Field Classes conducted by Dr. Wyman have attracted a record attendance in the past year. Conducted tours of the grounds are available to large groups requesting such service in advance. Many garden clubs took advantage of this service during the past year. The Massachusetts Horticultural Society had its regular field day at the Arboretum on May 15th, and four busloads of visitors attending the National Convention of the American Society of Landscape Architects were conducted through the grounds by members of the staff.

The ground cover and small tree display plots at the Case Estates in Weston are proving to be of increasing interest to visitors. Classes from four different colleges in New England made trips to Weston to study these collections. An experiment in the use of maleic hydracide and Crag herbicide is under way at the Case Estates. Preliminary results indicate that these materials may be valuable in reducing the hand labor required in the Arboretum as well.

Cytogenetics:

A number of new hybrid ornamental apples produced at the Arnold Arboretum have proved to be outstanding and are being propagated for distribution. The hybrids with *Malus Sargenti* are of special interest because of their dwarf habit and brilliant foliage during the spring and early summer. The hybrids, like the *M. Sargenti* parent, are facultatively apomictic and tend to breed true from seed.

Species hybridization is common in the subfamily *Prunoideae* (Rosaceae), and a number of spontaneous hybrids between *Prunus Besseyi* and other species have been found. An excellent example of the stability of the genus is shown in the artificial cross between *P. Besseyi* of central North America and *P. tomentosa* from eastern Asia. Although these species differ in many characters and have been separated for hundreds of thousands of years, they cross readily and the F1 hybrid is fertile.

The "Merrill" Magnolia, a hybrid produced fifteen years ago, has proved to be vigorous and early-flowering. It became available to the horticultural public from commercial sources in the spring of 1954.

Dwarfing rootstocks and bark inversion are being used for the development of dwarf ornamental trees. The bark inversion technique is being used to induce early flowering in ornamental trees and vines which are reluctant to produce flowers.

Hally J. Sax (Mrs. Karl Sax), utilizing the extensive living and herbarium collections of the Arboretum, completed a cytotaxonomic study of the genus *Cotoneaster*. Most of the species were found to be apomictic triploids. There is some evidence of facultative apomixis in these triploid species. Thus the species is able to perpetuate hybrid complexes through apomixis, yet retain some genetic plasticity to meet new environmental conditions by occasional hybridization.

Dexter Sampson, a graduate student, continued his work on the cytological analysis of the progeny from triploid hybrids in *Philadelphus* and *Forsythia*. Bradford Johnson, another graduate student, began a study of the cytology of facultative apomixis in *Malus*.

Comparative Morphology:

Professor Bailey has completed his task of preparing material for publication in book form by the Chronica Botanica Company. This volume which deals with salient trends of anatomical research during the period 1909–1953 will be released for sale in the near future. Miss Margery P. F. Marsden has completed her intensive investigation of *Clerodendron trichotomum* Thunb. and received the doctorate from Radcliffe College in June. Mr. Chi Ling Chen developed symptoms of tuberculosis early in the fall and is having to spend at least a year at the State Sanatorium in Rutland. This was extremely unfortunate, not only in postponing completion of his work on the Sapotaceae for the doctorate, but also in depriving Professor Bailey of his expert assistance in preparing the wood collection for transfer to its quarters in the new botanical building.

The wood collection was initiated by Professor Sargent during the early years of his administration of the Arnold Arboretum. It has subsequently been enlarged and strengthened by additional accessions at the Arnold Arboretum and by successive contributions made by the Forestry School, the Bussey Institute and the Department of Biology. Since 1936, it has been housed, as have staff members of the Arnold Arboretum concerned in its use, in the Biological Laboratories without cost to the Arboretum. For a number of years the Department of Biology provided financial assistance in the making of catalogues and microscopic slides. Furthermore, Professor Wetmore and his associates contributed much time and effort to expanding and improving the collection. In transferring the much enlarged collection, new steel cases and many new trays have been provided by the University. The Biological Laboratories also generously contributed a large number of the trays in which the collection was formerly stored. In its new quarters, the collection is housed in close proximity to the collections of fruits and seeds and slides of pollen, leaves and flowers. Thus, any taxonomist working with herbarium specimens now has efficient and convenient access to supplementary data contained in these extensive and very valuable collections.

The Herbarium:

The activities of the herbarium staff during the past year were involved in the preparations to implement the vote of the Harvard Corporation. The Curator, Dr. Kobuski, and Miss Perry devoted regular time and many extra hours to the designation and separation of the horticultural herbarium and the preparation of the non-horticultural material for the move. In spite of these steps of preparation, the regular activities continued in the herbarium. During the past year 3560 specimens were mounted and added to the herbarium, which now contains 675,119 sheets. A total of 12,421 specimens were sent out in exchange, 11,121 to foreign institutions and the remainder to American herbaria. New collections received at the Arboretum number 27,758 specimens. Of these, 12,000 specimens came as gifts or in exchange, while approximately 16,000 specimens were received from expeditions or collectors sponsored completely or in part by the Arnold Arboretum. Nearly 85% of the incoming materials were received from Malaysia and Asia, forming a significant addition to the valuable collections already in the Arboretum from this area. Among the noteworthy accessions are 14,000 specimens collected by L. J. Brass on his most recent trip to New Guinea; Richard Schultes' collection of 3,500 specimens from the Amazon; 2,000 specimens from the Philippine Bureau of Science collected in oriental Mindoro, and 3,500 specimens from Japan, the Ryukyu Islands and other accessible areas of Asia. An active exchange continues between the Bogor Herbarium in Java and the Arnold Arboretum. During the past year the Arboretum received 2,400 specimens from the Bogor Herbarium collected in various regions of Indonesia.

The number of requests for loans of specimens from the Arboretum

collections continues high. A total of 5,457 specimens were sent out on loan during the year to twenty-two different institutions. Foreign requests for loans numbered eleven.

During the year, staff members conducted research on plant families and areas of their specialties. Dr. Howard was appointed Senior Botanist on a project sponsored by the Institute of Jamaica in Kingston, Jamaica, British West Indies, to survey the native vegetation on bauxite soils on that island. The project hopes in the course of this work, to determine what plants of potential economic value can be grown on mined-out bauxite areas. Dr. Howard continued his work on the vegetation of the Caribbean Islands and made some progress on monographic studies of the genus *Coccoloba*.

Dr. Kobuski continued his work on the Asiatic members of the *Theaceae* and specifically towards a treatment of this family for the Flora Malesiana. He also identified several large collections of this family for various herbaria.

Dr. Johnston concentrated on his studies of the *Boraginaceae*, with a special interest in the herbaceous genera found in Asia and the Middle East.

Dr. Perry continued her work on the New Guinea flora, giving special attention to the recently received collections of L. J. Brass.

Dr. Hu is completing a monographic study of the ornamental genus *Philadelphus* and supervises the initial stages of the preparation of a list of the species of flowering plants reported from China.

Dr. Merrill is now receiving the proofs on his book regarding the botany of Captain Cook's two voyages in the Pacific. It is expected that this major contribution will be published in the fall.

The Library:

The preparation and implementing of plans to organize a horticultural library and the separation of those books to be moved to Cambridge formed a major portion of the work of the librarian and the library staff during the past year. The Corporation requested in its vote that all Arboretum books to be housed in Cambridge be distinctly marked. Thus, within the past year all books which are part of the Arboretum library have been checked and marked where need be, with a stamp or sticker on the back, an embossed imprint within the pages, or a bookplate, or a combination of these. An excellent selection of books of horticultural use was made with the cooperation of Dr. Wyman and other members of the staff. These books to remain in Jamaica Plain will eventually be located in a newly designed library and reading room on the first floor of the Administration Building, with room for expansion or for little used volumes on the second floor of the herbarium wing.

Additions to the library by gift, purchase or binding totaled 271 volumes. The library now contains 48,673 bound volumes on the shelves. Pamphlets numbering 206 were added to the pamphlet collection, bringing that collection to a total of 15,410 items. Five hundred and four

catalogue cards were added to the main catalogue and 1206 cards were added to the Gray Herbarium index of American species. Inter-library loans showed an increase over past years, although many additional requests were answered by typing short descriptions, or through the use of microfilm and photostat copies.

Exhibits and Displays:

The Larz Anderson Collection of Japanese Dwarf Trees was featured at the exhibit of the Arnold Arboretum at the Spring Flower Show of the Massachusetts Horticultural Society. The plants were exhibited in a setting of a Japanese garden. An interesting bamboo shelter was erected to shelter these plants in a fashion comparable to that used in Japan. Three excellent Kurume azaleas loaned by Mr. John Ames added color to the display. A first prize and a gold medal were won by this display.

Several additional displays of living plant materials were furnished for other shows of the Massachusetts Horticultural Society during the year. An Arboretum display of sprays of flowers, tree photographs and Ektachrome display panels occupied a featured location at the National Convention of the American Society of Landscape Architects at the Hotel Somerset. This exhibit attracted much attention and was mentioned in the programs and news releases of the meetings.

Publications:

Four issues of Volumes 34 and 35 of the Journal of the Arnold Arboretum were issued quarterly totaling 522 pages. Dr. Kobuski serves as editor of the Journal, assisted by an editorial board of other members of the Arboretum staff. Twelve numbers of Arnoldia were issued under the editorship of Dr. Wyman and were distributed to the Friends of the Arnold Arboretum and additional subscribers so that the total distribution now numbers 2,200. The subscription price of Arnoldia was raised to two dollars per year. This represented the first increase in price since this publication first appeared. A demand for back numbers of Arnoldia increased to the point where it seemed desirable to accept an offer of the D. Van Nostrand Company of New York to publish some of these as "The Arnold Arboretum Garden Book." Some forty-five issues were selected and Dr. Wyman wrote an introduction and foreword for this book. Proof of the book is now being received and publication is expected in the fall of 1954.

Gifts and Grants:

The Arboretum is fortunate to receive a large number of gifts from individuals interested in the work of the organization and the staff. Most of these are received as "memberships" in the "Friends of the Arnold Arboretum." During the past year 431 memberships were received. Such gifts are assigned, unless otherwise designated, to a fund called "gifts for cultural purposes" and are used exclusively to sponsor additional work

on the grounds, such as developing new collections, additional care for the plantings or for research and work leading to the development of new hybrids, dwarf plants and similar projects. Additional gifts were received designated for specific purposes. One gift from a Friend of the Arboretum was to be used to support foreign collectors and thereby obtain for the Arboretum additional material of horticultural value. It is hoped that this meritorious fund can be increased in future years. Another large gift was placed at the discretion and joint use of Dr. Reed Rollins, Director of the Gray Herbarium and Dr. Howard, Director of the Arboretum, to be used for research in systematic botany for the benefit of both the Arnold Arboretum and the Gray Herbarium.

The Arboretum received a bequest from the estate of Emery Holden Greenough which was assigned to the endowment of the Arboretum. Through the generosity of Mrs. Martha Peters, her home and the land thereabout on South Street was given to the Arboretum. It is hoped that eventually when funds are available the setting of this old house can be used as a demonstration landscape area to show plants for small homes in a good setting. The adjacent land when reconditioned will be of great value to the Arboretum as a nursery area.

Numerous Friends have given books on plants and flowers to the Arboretum. The value of these books is determined by the librarian and reported to the donor for income tax purposes. Many of the books are welcome additions to the library, while others serve as replacements for worn books long in use.

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1953–1954

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